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Rhodora

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NEW ENGLAND BOTANICAL CLUB

Conducted and published for the Club, by

ALBION REED HODGDON, Editor-in-Chief

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Associate Editors

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COMPARISONS OF SEXUAL AND APOGAMOUS RACES IN THE FERN GENUS PELLAEA

ALICE F. TRYON

Apogamy in ferns is of the obligate type involving changes in the gametophyte eliminating fertilization by absence or non-function of the archegonia. This is correlated with a compensating system in the sporophyte, circumventing the reduction in chromosome number by changes in the mitotic or meiotic divisions in the sporangium, prior to spore formation. Thus both gametophyte and sporophyte stages have the same chromosome number. This synchronized apogamous system is particularly remarkable for it evidently has been independently initiated more than once in 25 of some 209 genera of the Filicopsida which are cytologically known.

This study in *Pellaea*, on some morphological modifications which are associated with apogamy, was made with the purpose of understanding the evolutionary role of the mechanism in this group, against a background of rapidly increasing information on the frequency of the phenomenon in the Pteridophyta.

Apogamous ferns are considered to be of hybrid origin by Manton (1950, 1961) and Walker (1966) and there is support for this view in the following survey of chromosome levels and the apogamous condition. Data are drawn from the reports of chromosome numbers in the Filicopsida by Chiarugi (1960) and Fabbri (1963, 1965). An analysis of these records shows apogamy in 32 diploids in 9 genera,

66 triploids in 15 genera, 15 tetraploids in 6 genera, 5 pentaploids in four genera and one hexaploid and one octoploid. About 73% of these apogamous forms are at polyploid levels while 27% are apparent diploids, although the latter may not represent base numbers of the genera. The large proportion of apogamous forms at polyploid levels supports the hypothesis of a relationship of apogamy with hybridization. However, the percentage of diploids is a significant one and the origin of apogamy in these is not apparent.

In some genera, as *Pteris*, apogamy is especially frequent, and it is reported by Walker (1962) in 16 diploids, 14 triploid and 9 tetraploid forms. In *P. cretica* apogamy occurs in diploid, triploid and tetraploid forms and it also occurs in *P. biaurita* at diploid and triploid levels and in triploids and tetraploids in *P. quadriaurita*. In *Adiantum*, apogamy is reported in five diploid, three triploid and one hexaploid member. In *Dryopteris* five diploids and 16 triploids are apogamous, and in *D. Borreri* it is known at diploid, triploid, tetraploid, and pentaploid levels. In contrast to these, there are some large genera such as *Asplenium*, in which apogamy is infrequent with reports of only three triploid, one pentaploid, and two octoploid members, and it is not, or doubtfully, reported in *Blechnum*, *Cyathea* and *Thelypteris*. Thus, while apogamy is prevalent in some groups and absent in others it is notable that it occurs in a number of genera which are only distantly related.

Some information on the origin of apogamy in ferns comes from experimental studies on induced apogamy in gametophytes in which there appears to be a genetic predisposition for the condition. In these, apogamy is influenced by environmental changes such as drying, light intensity and in increased concentration of certain sugars. In some of these studies, as those by Whittier (1964), it is recognized that the induction of apogamy is more readily accomplished in certain "races" of a species than in others. The genetic control of apogamy as a dominant is demonstrated by experiments on *Pteris* by Walker (1962) where crosses made

between apogamous diploids and sexual species produce only apogamous forms. Dominance may be effective in perpetuating and increasing the number of apogamous forms by crosses involving antherozoids from apogamous plants. This may account for the frequency of apogamy in certain groups as *Pteris, Adiantum* and *Pellaea.*

There have been several studies of apogamy in *Pellaea* and it is known in six of the 15 species in section *Pellaea.* The triploid species *P. atropurpurea,* reported by Manton (1950) and a triploid variety in *P. sagittata,* noted by Tryon & Britton (1958) appear to be of hybrid origin. Apogamy is reported here in three species of section *Pellaea* belonging to the "light-stiped" group which represent a separate evolutionary line in the section. This record of apogamy in a distinct species-group is in harmony with reports of its occurrence in different genera and is indicative of independent origins of the mechanism. These three closely related species — *P. andromedifolia* (Kaulf.) Fée, *P. intermedia* Mett. ex Kuhn and *P. ovata* (Desv.) Weatherby — are exceptional in the ferns for each has both sexual diploid and apogamous triploid races. The triploid chromosome level of the apogamous types shows a relationship to hybridization. The morphological similarity of the sexual and apogamous races in each of the species is suggestive of a close relationship between the putative parents. Comparative studies were made of the chromosome numbers, gametophytes, juvenile leaves, guard cell size and spore size for the two forms in each species. Comparisons are also drawn with a sexual diploid and sexual tetraploid in *P. ternifolia* (Cav.) Link var. *ternifolia* (later referred to by the species name only), also a member of Section *Pellaea* but belonging to a "dark-stiped" group, as a basis for comparison of polyploidy without apogamy. Geographic distributions of the races are compared as a measure of the evolutionary success of the different forms. Most of the apogamous members in Section *Pellaea* are widely distributed in North America or also South America while most sexual members have more limited ranges.

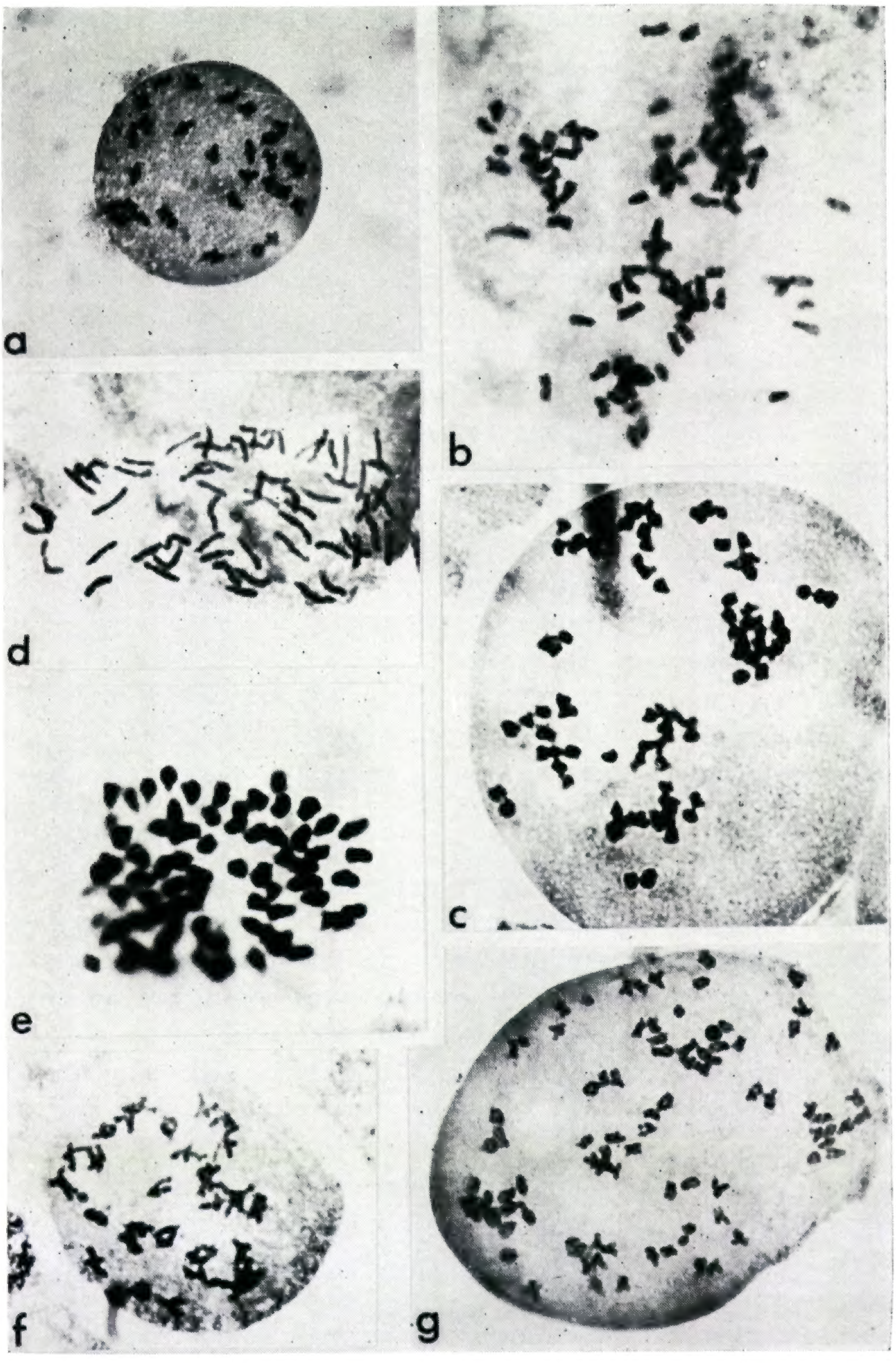

Fig. 1. a-c. *Pellaea andromedifolia,* squash preparation of meiosis. a. Sexual diploid, n = 29, San Gabriel Mts. Calif., × 650. b. Apogamous triploid, "n" = 87, Humboldt Co., Calif., × 1650. c. Apogamous

Material and Methods

Measurements and cytological reports in this study were obtained from original collections, or plants grown from spores obtained from them, maintained in a greenhouse for a period of two to six years. Field studies and collections were made with R. M. Tryon in the western United States and Mexico in 1950, 1956 and 1957. Collections from the first trip are deposited at the Missouri Botanical Garden. Some duplicates of these, those from the last two trips, as well as cytological vouchers, are deposited at the Gray Herbarium. Meiotic chromosome counts reported here were obtained by the standard fixation in 3:1 alcohol and acetic acid and stained in acetocarmine as described by Manton (1950). The same fixative and stain were used for the mitotic cells from root tips and this material was treated with snail cytase following the procedure reported by Fabergé (1945). The snail enzyme breaks down the middle lamella and allows the chromosomes to spread freely when pressure is applied.

Distribution records were plotted from specimens deposited at the Gray Herbarium, the New York Botanical Garden, the United States National Herbarium, the California Academy of Sciences, Pomona College, Rancho Santa Ana Botanic Garden, San Diego Natural History Museum, Stanford University and the University of California, Berkeley.

Comparisons of Apogamous and Sexual Forms

Chromosome Numbers

Plants of the sexual type of *Pellaea andromedifolia,* from the San Gabriel mountains in southern California *(Alt 3)* and from Humboldt County in northern California *(Tryon & Tryon 5557)* have the normal complement of 16 spore mother cells and show at diakinesis that $n = 29$ with com-

triploid, "n" = 87, Point Mugu, Calif., × 1300. d-e. *P. intermedia,* d. Mitotic cell from root tip, 2n = 58, Saltillo, Mexico, × 1300. e. Squash preparation of meiosis, apogamous triploid, "n" = 87, Chiricahua Mts., Arizona, × 2500. f-g. *P. ovata,* squash preparations of meiosis, f. Sexual diploid, n = 29, Gillespie Co., Texas, × 2000. g. Apogamous triploid, "n" = 87, San Luis Potosí, Mexico. × 650.

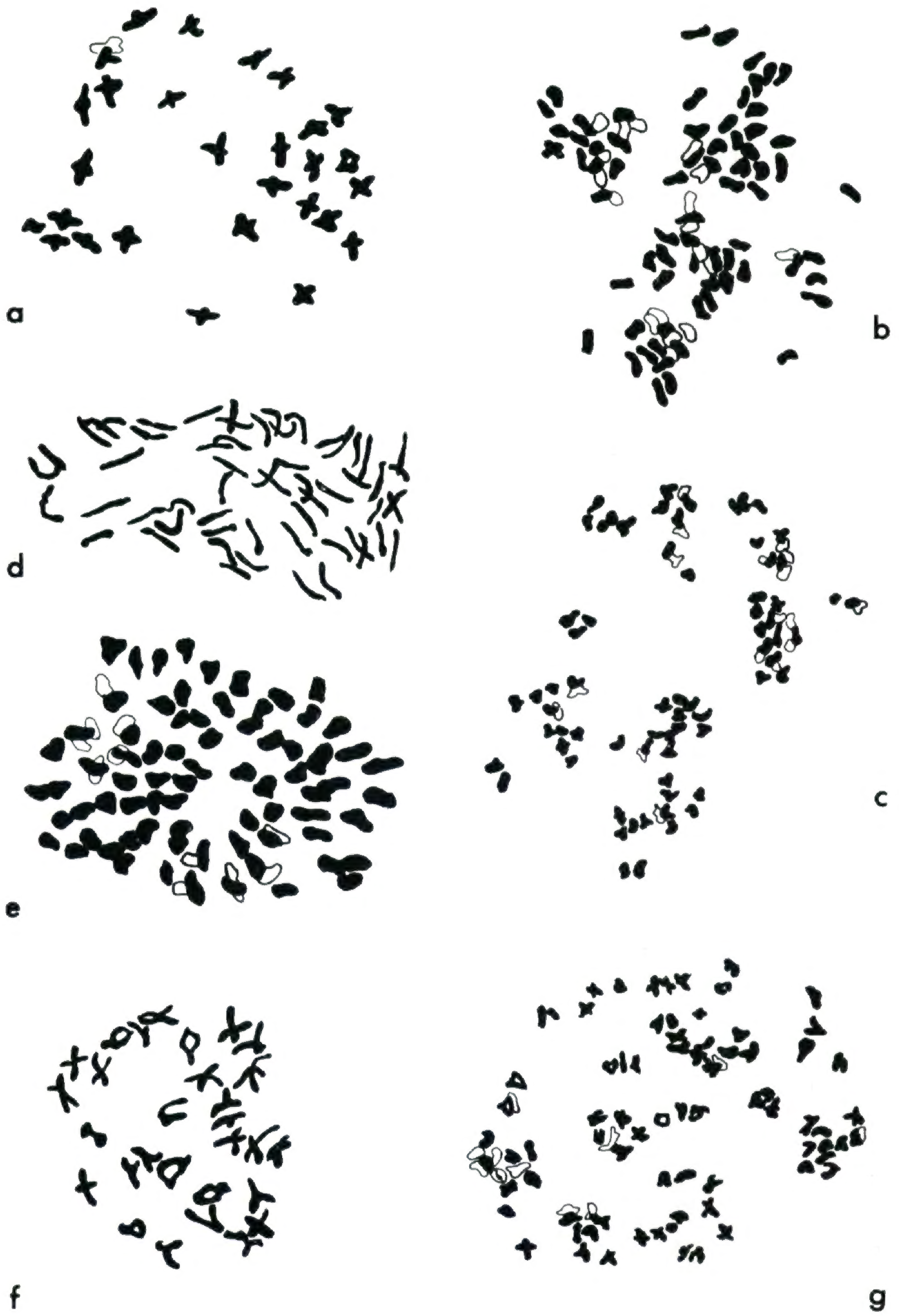

Fig. 2. Explanatory, enlarged diagrams for Fig. 1 showing chromosomes in focus in black and white and the remainder in outline. a-c. *Pellaea andromedifolia*, a. Sexual diploid, n = 29. b. Apogamous

plete and regular pairing (Figs 1a, 2a). Apogamous plants from Humboldt County in northern California *(Harris 21651)* resemble the sexual plants in leaf morphology, have sporangia with eight spore mother cells and at diakinesis show that "n" = 87 with complete and regular pairing of the chromosomes (Figs. 1b, 2b). Apogamous plants from Ventura County in southern California *(Kiefer 1132)* differ from apogamous plants from Humboldt County in having narrower leaves and pinnae of a more coriaceous texture. They have eight spore mother cells per sporangium and at diakinesis "n" = 87 with the chromosomes completely paired (Figs. 1c, 2c).

Plants of *Pellaea intermedia* grown from a collection from northern Mexico, east of Saltillo *(Rollins & Tryon 58144)* have 64 spores per sporangium. Mitotic cells from the root tips show chromosome figures of $2n = 58$ (Figs. 1d, 2d). Apogamous plants, morphologically similar to the sexual ones, grown from a collection from the Chiricahua mountains in southern Arizona *(Tryon & Tryon 5089)* show "n" = 87 at diakinesis and complete pairing (Figs. 1e, 2e). No 16-celled sporangia were observed.

Plants of *Pellaea ovata* of the sexual type which were grown from a specimen collected in Gillespie County in central Texas *(Tryon & Tryon 5029)* have the normal complement of 16 spore mother cells and the haploid chromosome number is — 29 (Figs. 1f, 2f). Apogamous plants grown from a collection from northern Mexico, near San Luis Potosí *(Rollins & Tryon 58222)* in leaf morphology closely resemble plants of the sexual type; only eight spore mother cells were observed and at diakinesis "n" = 87 chromosomes (Figs. 1g, 2g).

These cases of apogamy in triploid plants of *Pellaea* are similar to the classic example reported for *Pellaea atropurpurea* by Manton (1950) and also by Tryon and Britton

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triploid, "n" = 87. c. Apogamous triploid, "n" = 87. d-e. *P. intermedia,* d. Sexual diploid, 2n = 58. e. Apogamous triploid, "n" = 87. f-g. *P. ovata,* f. Sexual diploid, n = 29. g. Apogamous triploid, "n" = 87.

(1958) in *P. sagittata.* They are, however, unique in the occurrence of both sexual diploids and apogamous triploids which are of generally similar morphology, in each of the species. In *P. sagittata* the diploid var. *cordata* and the triploid var. *sagittata* are morphologically distinct — and in *P. atropurpurea* the triploid is the only known form. In these apogamous taxa, the problem which Manton alluded to as the "triploid dilemma" was explained in the case of *P. atropurpurea* as possibly arising as a back-cross between an allotetraploid and one of its diploid parents, largely on the basis of pairing relationships in the 16-celled sporangia.

In the three species reported here each sexual diploid form has most probably served as a parent in the cross producing a morphologically similar triploid. The second parent might be a tetraploid as suggested by Manton or possibly an autotetraploid originating from different races of the same species. Tetraploids are not known in these three species although they are known in the section and two of these are apogamous. Another possible parent is an apogamous diploid, as was reported in the formation of apogamous triploids in *Pteris* by Walker (1966). Plants of this constitution are not known in *Pellaea.* This record of both sexual diploid and apogamous triploid plants in three closely related species is of special interest for it appears that the parental forms in each of them share a capacity for generating the synchronized mechanism necessary for obligate apogamy.

Gametophyte and Juvenile Leaves

Illustration of the sexual and apogamous forms for comparisons of these stages in the life history is shown in *Pellaea andromedifolia* (Fig. 3). More detailed accounts of particular structures have been made by Atkinson, in Tryon and Britton (1958), Tryon (1960) and Nayar and Bajapi (1964).

Spores of both sexual and apogamous types germinate rapidly, usually between 6-15 days, and the prothallia also develop quickly with as many as 26 cells and a small plate in ten days. The mature structure is cordate and erect. In

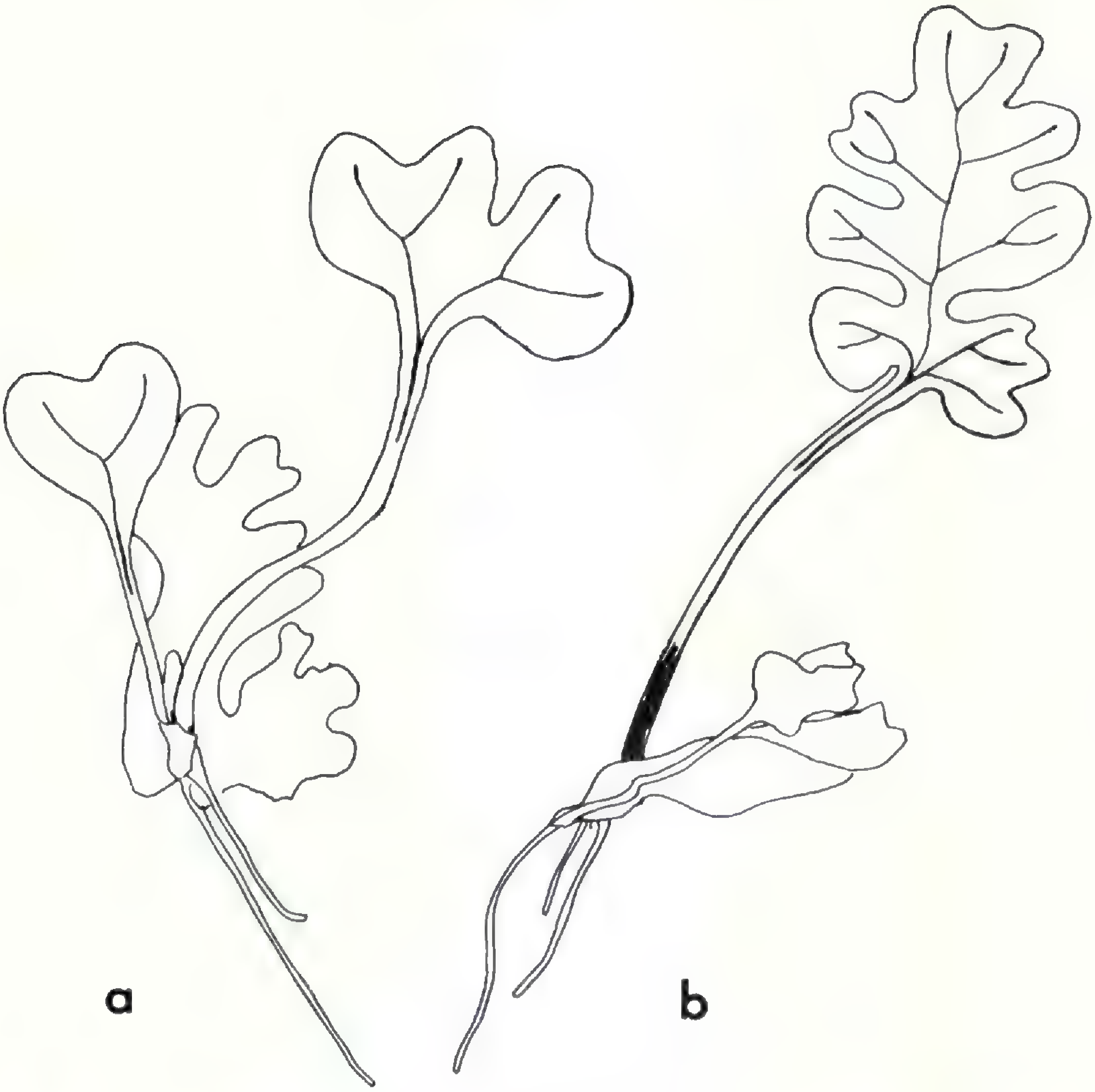

Fig. 3. Tracings of gametophytes and juvenile leaves of sporophytes, of *Pellaea andromedifolia*, at 6 months, × 5. a. Sexual diploid, gametophyte at base with several irregular lobes and the first two symmetrically lobed leaves of the sporophyte, from *Tryon & Tryon 5557*. b. Apogamous triploid, gametophyte and early leaf of sporophyte at base, the fifth leaf with deep, asymmetrical lobes, from *Tryon & Tryon 5556*.

the *sexual type* antheridia are produced first, usually after 15 days, and may be formed on plants with as few as 20 cells. They are confined largely to the lower surface in the posterior region, nearest the spore, and are abundant among the rhizoids. Archegonia are formed later than the antheridia, on a cushion of cells 2 or 3 layers thick, on the lower surface in the anterior region, a few cells behind the central notch. Among the rhizoids of large prothallia there may

be several small prothallia bearing only antheridia. These seem to be of the form recognized by Stokey (1951) as ameristic and their development may promote outcrossing in these plants. Juvenile leaves on sexual plants have symmetrical lobes; the initial ones bilobed and later ones with more and deeper sinuses (Fig. 3a). The prothallus may persist after the formation of several leaves with continued production of antheridia on new lobes. The *apogamous type* germinates slightly earlier than the sexual one. One or both sex organs may be suppressed but usually antheridia are formed. Antherozoids are abundantly produced and appear normally developed. Archegonia are usually absent but non-functional ones were observed in *P. andromedifolia*, after young "embryos" were developed. "Embryos" develop, independent of sex organs, after two or three months, usually in the central portion of the prothallus, adjacent to the notch. They may be surrounded by slender, hyaline scales attached to the prothallus and young leaves. The first leaves of apogamous plants are often asymmetrical, and pinnate leaves resembling the mature form are produced earlier than on sexual plants (Fig. 3b). The different time of development and morphology of these structures in the apogamous forms appear to represent a repatterning of the similar growth systems in the sexual forms.

Precise ecological data are lacking for most collections of these species; however, in Humboldt County, California where both sexual and apogamous plants of *P. andromedifolia* grow together; the apogamous ones grow among rocks in exposed situations and the sexual often grow in humus in more shaded sites. The apogamous condition, eliminating the need for fertilization, would be advantageous to these species in occupying more xeric habitats. The evolutionary potential of the apogamous type is indicated by its adaptation to a different ecological niche.

Epidermis — Stomatal Guard Cell Size

The epidermal cells are of particular interest in these species since there is a correlation between the apogamous, polyploid condition and larger guard cell size. The epidermal

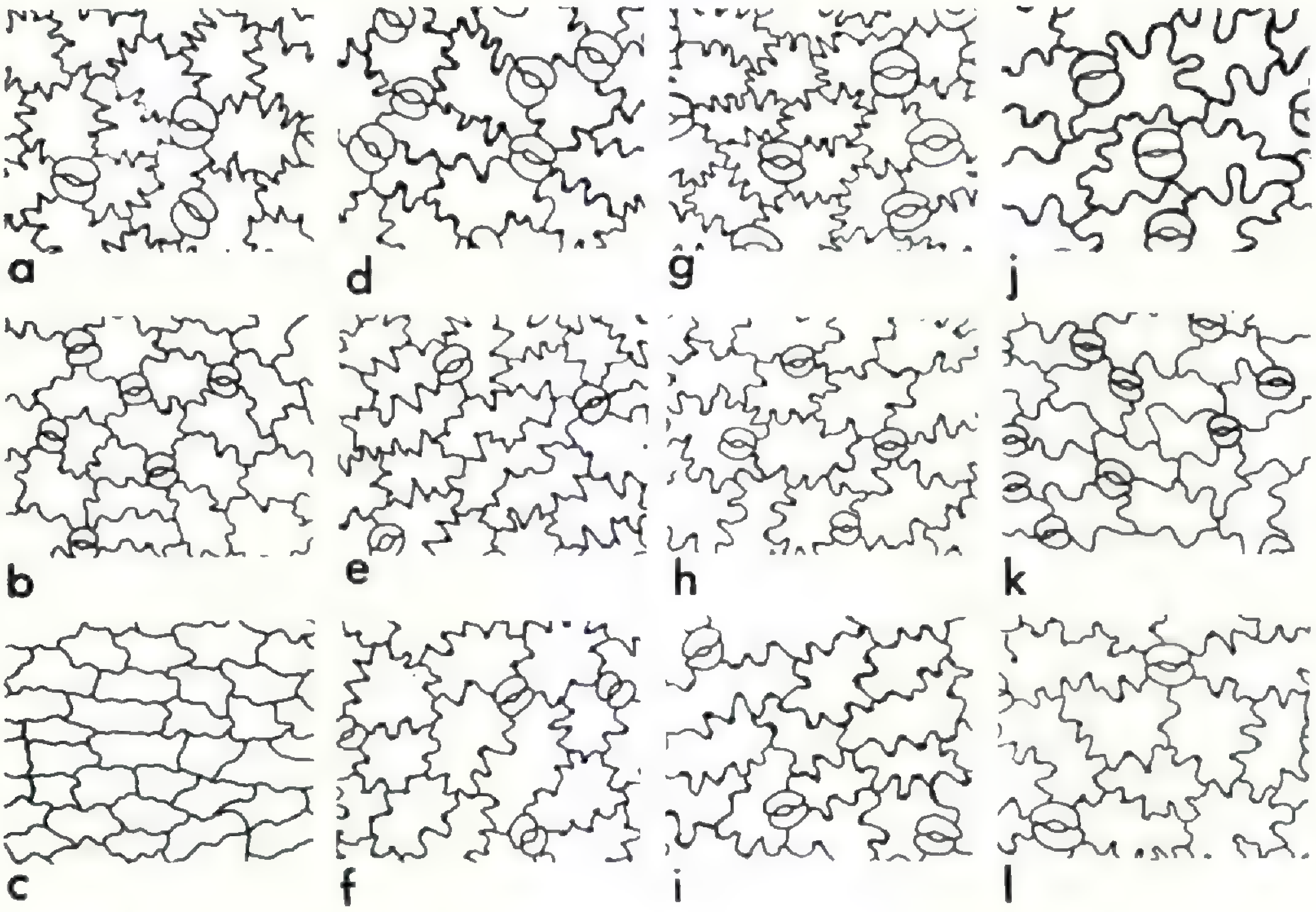

Fig. 4. Tracings of epidermal cell walls in *Pellaea*, × 80, of the abaxial surface with stomata, except c, adaxial surface. a-c. *Pellaea ovata*. a. 3×, *Correll 22792*. b. 2×, *Tryon & Tryon 5029*. c. 3×, *Rollins & Tryon 58222*. d-f. *P. andromedifolia*. d. 3×, *Harris 21651*. e. 2×, *Alt 3*. f. 2×, *Tryon & Tryon 5557*. g-h. *P. intermedia*. g. 3×, *Tryon & Tryon 5089*. h. 2×, *Rollins & Tryon 58144*. i. *P. myrtillifolia, Wagenknecht 946*, Chile. j-k. *P. ternifolia*. j. 4×, *Tryon & Tryon 5141*. k. 2×, *Tryon & Tryon 5105*. l. *P. rufa, Schelpe 4939*, South Africa.

cells of the abaxial surface, are photosynthetic and the guard cells which are confined to this surface, may develop against either one or two walls of the stomatal initial and are densely packed with chloroplasts. In the three species in *Pellaea* examined the abaxial epidermal cells have peculiar anticlinal walls that are sharp-angled with irregularly thickened peaks and sinuses. This is one of the features, along with the slender, creeping rhizome with bicolorous scales and small, ovate segments, characterizing these three species and two others allied to *P. andromedifolia*. Tracings of the walls from a microprojector are illustrated (Fig. 4) for all five species in this group and also for *P. ternifolia* representing

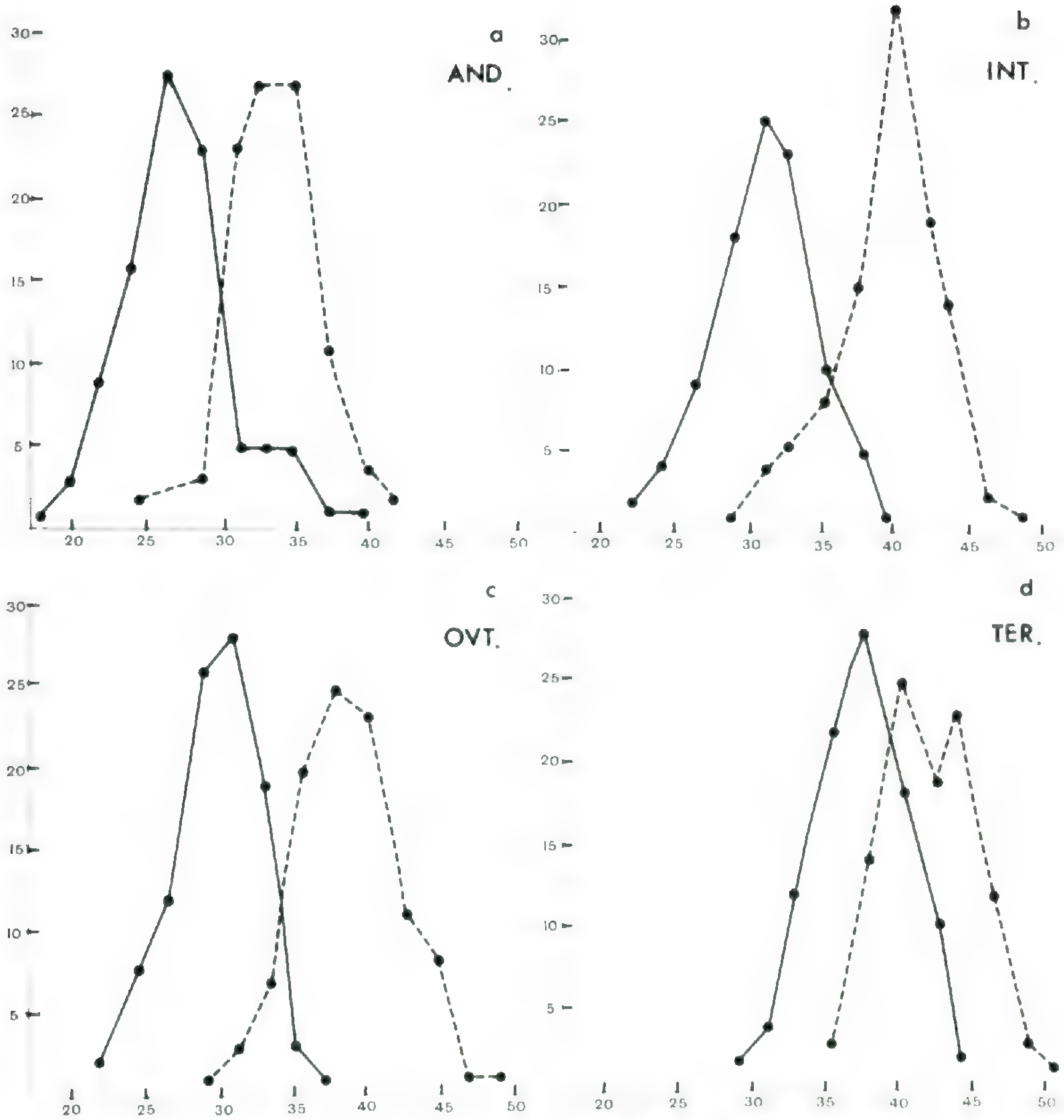

Fig. 5 a-d. Length of longer guard cell in 100 stomata; abscissa-guard cell length in micra; ordinate-frequency and %. a. *Pellaea andromedifolia*, solid line, sexual diploid, *Tryon & Tryon 5557;* broken line, apogamous triploid, *Tryon & Tryon 5556.* b. *P. intermedia*, solid line, *Rollins & Tryon 58144;* broken line, apogamous triploid, *Tryon & Tryon 5089.* c. *P. ovata*, solid line, sexual diploid, *Tryon & Tryon 5029;* apogamous triploid, *Rollins & Tryon 58222.* d. *P. ternifolia*, solid line sexual diploid, *Tryon & Tryon 5105;* broken line, sexual tetraploid, *Tryon & Tryon 5141.*

another group in the genus. The greater size of the guard cells in the apogamous and polyploid plants in the top row, compared to those in the center row, can be readily seen. The pattern of epidermal cells on the adaxial surface is also

illustrated for *P. ovata* (Fig. 4c). These have a different form with shallowly undulate walls, which are uniform in thickness and the cells are mostly longer than broad. In Fig. 5 a-c measurements showing the guard cell length are based on the larger member in each of 100 stomata, for both sexual and apogamous plants, plotted to the first decimal. In each species these illustrate the smaller guard cell size in the sexual diploid race as compared to the apogamous triploid. In the text the ranges are given by summation to the nearest whole number. In *P. andromedifolia* the range in length of the guard cells (Fig. 5a) in a sexual diploid plant from northern California is 18-40μ, with a mean of 27. The range of an apogamous triploid plant from the same area is 24-42μ with a mean of 34, which is 26% larger than the sexual. In *P. intermedia* the range in guard cell length (Fig. 5b) of a sexual diploid plant from northeastern Mexico is 22-40μ with a mean of 31. An apogamous triploid plant from southern Arizona has a range of 28-48μ with a mean of 39, which is about 26% greater than the sexual type. In *P. ovata* the range in guard cell length (Fig. 5c) of a sexual diploid plant from central Texas is 22-37μ with a mean of 30. An apogamous triploid plant from north-central Mexico ranges from 29-48μ with a mean of 38, which is about 27% larger than the diploid.

The data from these apogamous and polyploid races may be compared with that from *P. ternifolia,* in which a sexual polyploid race is known. In Fig. 5d the measurements of the guard cells are given for a sexual diploid and for a sexual tetraploid of *P. ternifolia.* The sexual diploid plant from southcentral Mexico ranges from 29-44μ with a mean of 37. The sexual tetraploid from the same region ranges from 35-51μ with a mean of 42, which is 14% larger than the diploid. The increase in size of guard cells in the polyploid over the diploid in the sexual *P. ternifolia,* with a 1:2 ratio in chromosome number of diploid to tetraploid, is significantly less than the 26% or 27% increase in the apogamous polyploids over the other three species having a 2:3 ratio of chromosome number in the diploid to triploid

levels. This suggests that apogamy may be a factor in the increase in the size, augmenting, in these examples, the well known effect of polyploidy.

The epidermal patterns for two species of the group in which apogamy is not reported are also included (Figs. 4 i, 1). The average guard cell size of *P. myrtillifolia*, an endemic in north Chile, is 39μ and that in *P. rufa*, which occurs in the South African Karroo, is 38μ. The chromosome numbers are not reported but both species have the normal complement of 64 spores. The average size of the guard cells in these corresponds to that of the polyploid forms in the previous sets and suggests that they may be polyploid.

Spores

The apogamous condition in ferns is most readily detected by 32 spores per sporangium which is half the normal complement in most leptosporangiate species. In apogamous plants having well developed spores this number is consistent at either diploid, triploid or tetraploid levels. The mechanism accounting for this departure from the normal is the premeiotic doubling of chromosomes along with arrested cytoplasmic cleavage, prior to the formation of spore mother cells. These changes result in eight rather than the normal number of 16 spore mother cells.

The spores of both the sexual and apogamous forms in *P. andromedifolia*, *P. intermedia* and *P. ovata* are generally morphologically similar. They are tetrahedral-globose, trilete and, in amb, biconvex. They are pale yellow with excrescences in the outer layer of the spore wall forming rugae which fuse into irregular reticula. The rugae are irregular, flattened and wing-like in surface view and appear as moderately sharp projections in profile. Three commissural ridges protrude slightly from the surface and extend to the equatorial region. However, spores of apogamous plants differ from those of sexual plants in having more numerous and more prominent rugae as well as a larger size and a smaller number per sporangium. Spores of apogamous plants may also show marked variation in the form of the commissural ridges. They may be

trilete, as in spores of sexual plants, or they may have only a single ridge or a dense rugose patch asymmetrically placed on the proximal face. The monolete spores which frequently occur in apogamous plants appear to become dissociated from the tetrad early in their development.

Measurements of the greatest diameter of 100 spores from plants of each of the races of these three species are presented in graphs (Fig. 6 a-c). In these, size has been plotted to the first decimal. In the text the decimal has been elminated by summation to the nearest whole number. In *P. andromedifolia* the range in spore size (Fig. 6a) of

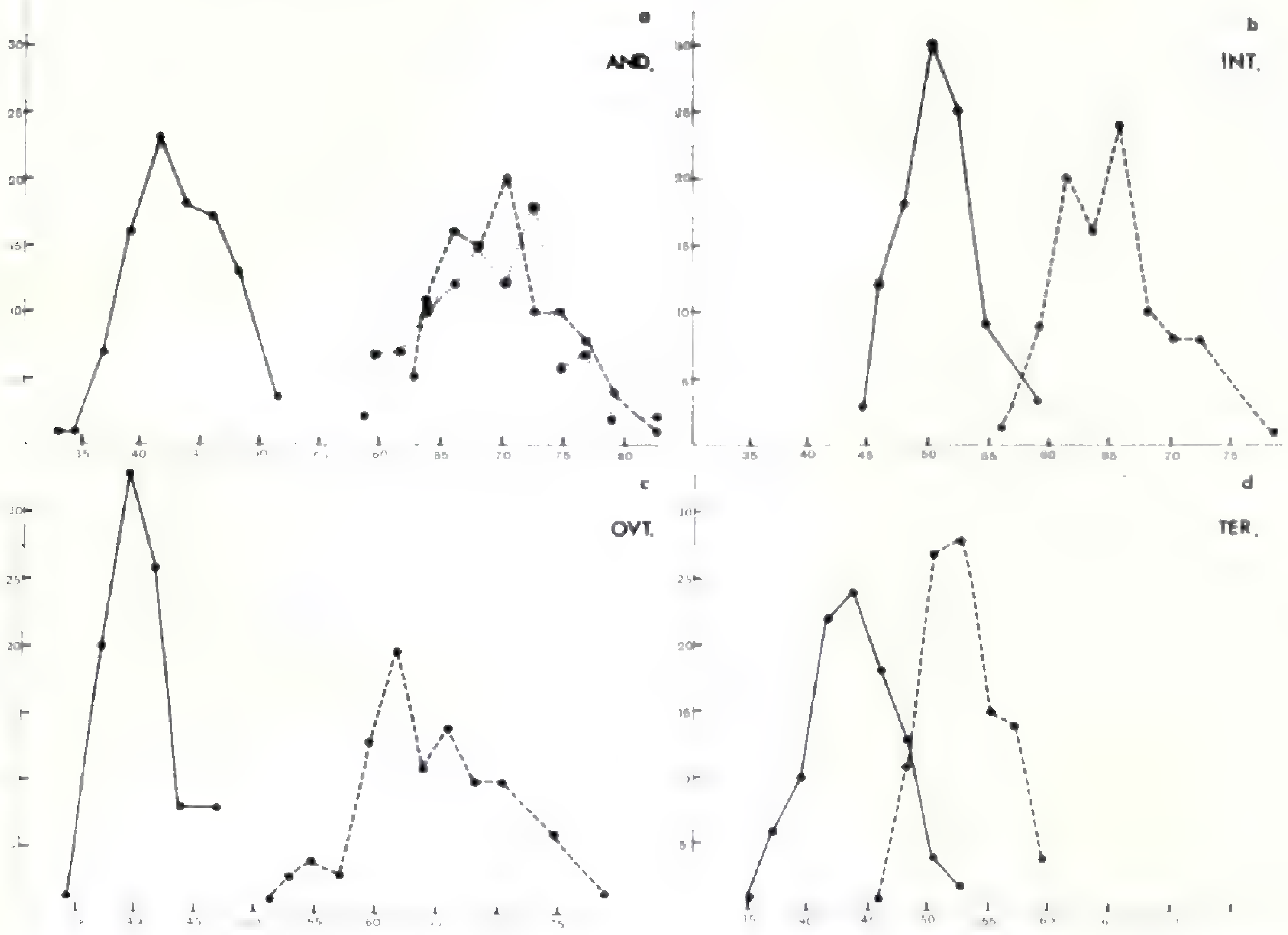

Fig. 6 a-d. Length of longest diameter in 100 spores; abscissa-length in micra; ordinate-frequency and %. a. *Pellaea andromedifolia*, solid line, sexual diploid, *Alt 3;* dashed line, apogamous triploid, *Harris 21651;* dotted line, apogamous triploid, *Kiefer 1132.* b. *P. intermedia*, solid line, sexual diploid, *Rollins & Tryon 58144;* broken line, apogamous triploid, *Rollins & Tryon 58306.* c. *P. ovata*, solid line, sexual diploid, *Tryon & Tryon 5029;* broken line, apogamous triploid, *Rollins & Tryon 58222.* d. *P. ternifolia*, solid line sexual diploid, *Rollins & Tryon 58218;* broken line, sexual tetraploid, *Tryon & Tryon 5141.*

a sexual plant from southern California is is 34 - 52μ, with a mean of 44. Spores from an apogamous plant from the southern portion of the state range from 59 - 83μ, with a mean of 70 which is 59% larger than the sexual. Spores from an apogamous plant from the northern part of California range from 63 - 83μ and have a mean of 71 which is 61% larger than the spores of the sexual plant. In *P. intermedia* (Fig. 6b) spores of the sexual plant range from 44 - 59μ with a mean of 52, while those of the apogamous plant range from 56 - 79μ with a mean of 66, which is about 27% larger than those of the sexual plant. In *P. ovata* (Fig. 6c) spores of the sexual plant range from 34 - 47μ with a mean of 41 and those of the apogamous plant range from 52 - 79μ, with a mean of 66 (61% larger than the sexual plant). In the graphs illustrating these ranges in spore size, it may be seen that there is no or little overlap in sizes of the sexual and apogamous members in each of the three species. These appear in contrast to the graph showing spore sizes in *P. ternifolia* (Fig. 6d). Here spores from a sexual diploid plant range from 35 - 53μ with a mean of 44, while those of the sexual tetraploid range from 46 - 59μ, average 54 (23% larger), with a clear overlap. The influence of apogamy on the size of the spores is not evident. The ratios of cell size, based on chromosome level, in the diploid to triploid is 1 : 3 and of the diploid to tetraploid is 1 : 2. Thus the effect of apogamy on spore size is obscured by differences in the chromosome levels. The extent of variation in spore size of apogamous plants is clearly greater than that shown by the sexual plants. This contrasts with the condition in the sexual diploid and tetraploid and suggests that the process of spore formation is not as strongly controlled in the apogamous plants.

The larger spore size in the tetraploid *P. ternifolia* may be useful in distinguishing different cytotypes in the herbarium specimens. In the apogamous plants differences in spore number and size have utility in determining the ranges of cytotypes from herbarium material and such ranges may supply useful information on the geographic centers and migration of the species.

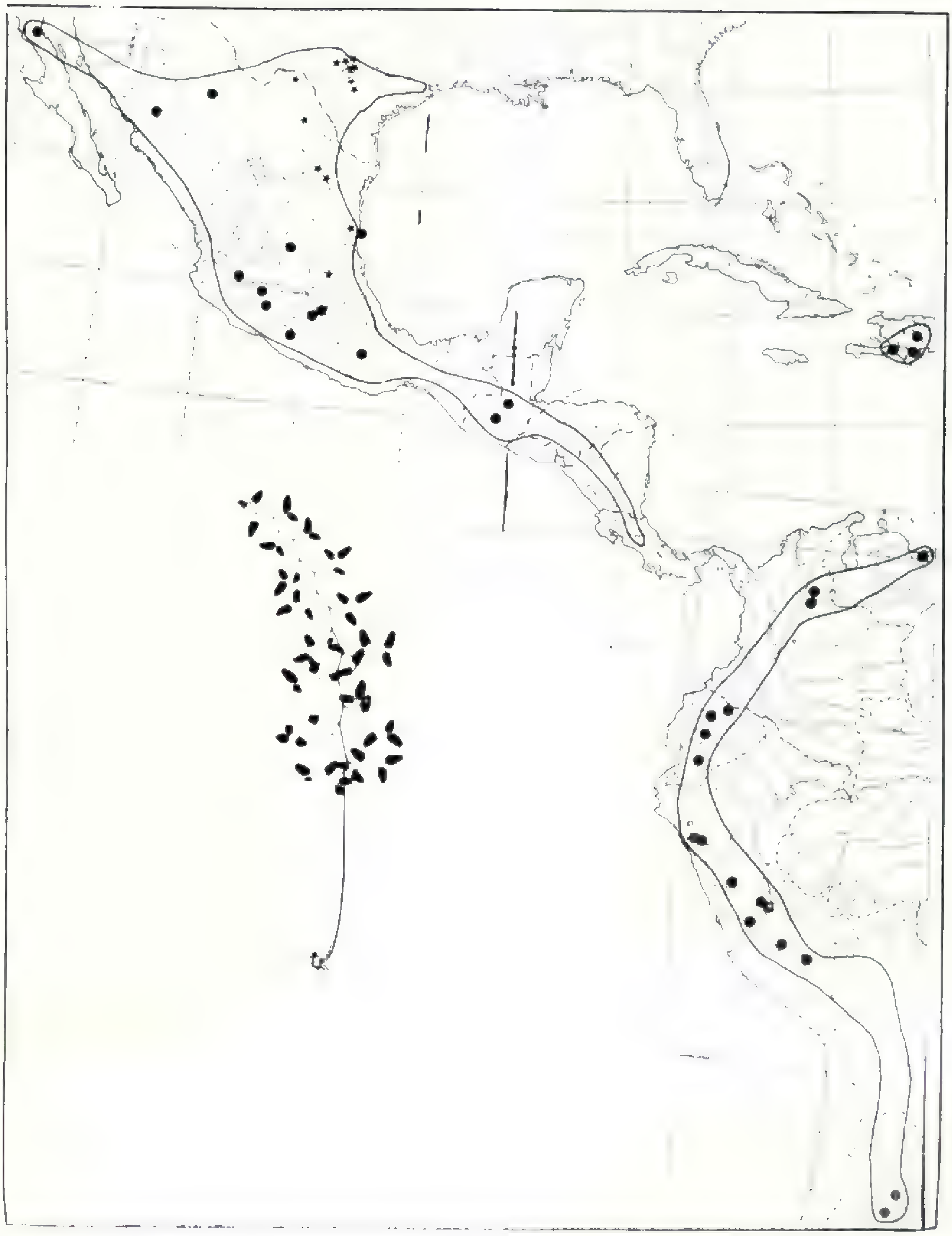

Fig. 7. Distribution of *Pellaea ovata* with leaf of sexual diploid (Fig. 1f) general distribution within solid line, stars at localities of 64-spored, sexual plants; dots at localities of 32-spored, apogamous plants.

Geographic Distribution

The general distribution of the species is shown in Figs. 7-9 by solid lines; the dots representing localities of

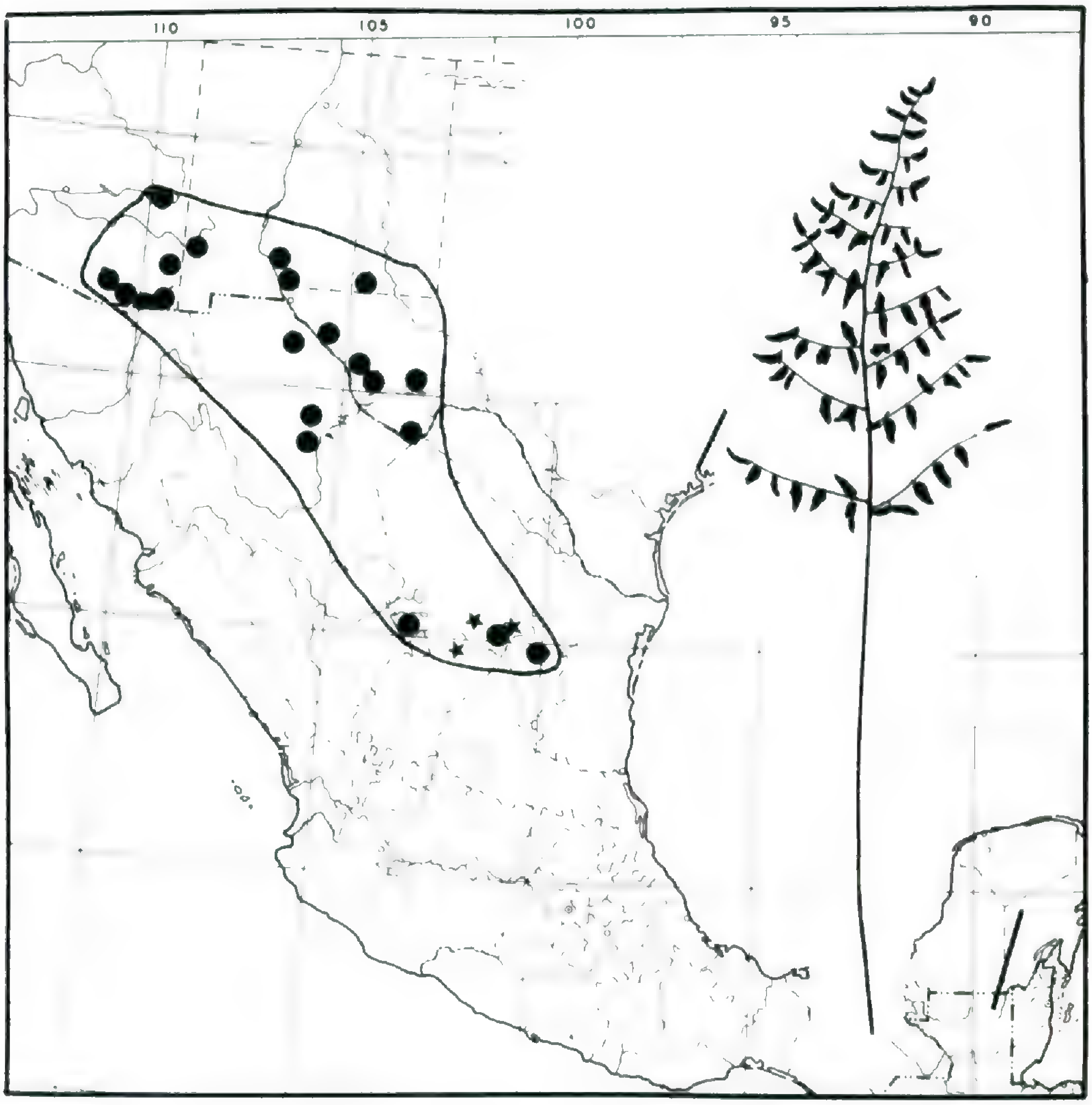

Fig. 8. Distribution of *Pellaea intermedia* with leaf of sexual diploid (Fig. 1d) general distribution within solid line, stars at localities of 64-spored, sexual plants; dots at localities of 32-spored, apogamous plants.

apogamous plants and stars the sexual ones, based on spore counts of material with sporangia intact. The silhouettes show the general shape of the leaves for each species and are taken from cytologically determined diploid plants. It is expected that additional material and field study will extend the ranges. However, these data are adequate to represent the general patterns. In these species, as in others where such distributions have been plotted, the apogamous races are generally more wide ranging. In *P. ovata* (Fig. 7), which has one of the most extensive ranges in the

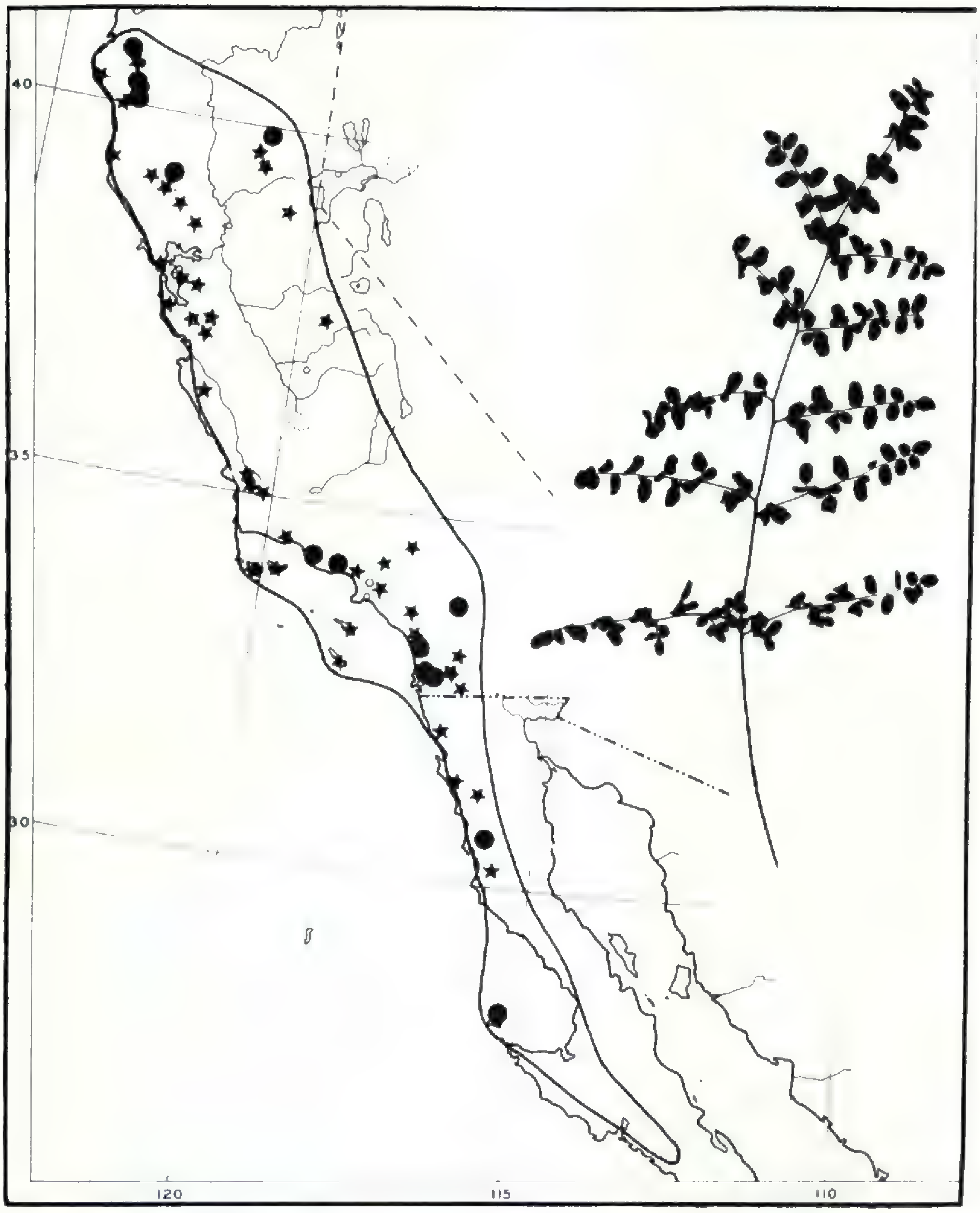

Fig. 9. Distribution of *Pellaea andromedifolia* with leaf of sexual diploid (Fig. 1a) general range within solid line, stars at localities of 64-spored, sexual plants; dots at localities of 32-spored apogamous plants.

genus, plants having the normal 64-spored sporangia are limited to central Texas and adjacent northeastern Mexico. All specimens from South and Central America, the Caribbean area and southern Mexico have 32 spores and are of

the apogamous form. The range of *P. intermedia* (Fig. 8) is restricted to the southwestern United States and adjacent northeastern Mexico. Plants with 32-spored sporangia are widely distributed in Texas, New Mexico, Arizona and northern Mexico while plants with 64 spores are known only from the region around Saltillo, Mexico. The distribution of sexual and apogamous plants in *P. andromedifolia* (Fig. 9) contrasts with the ranges of the previous species. Plants with 32 spores are disjunct, occurring in northern California in Humboldt County, and in southern California near Palm Springs and along the coast near San Diego south into Baja California and in adjacent Cedros Island. Both sexual and apogamous races occur within the same region and in Humboldt County they grow a few meters apart.

The ranges of the apogamous races of these three species may be compared with other apogamous pellaeas to provide a broader basis for an evaluation of the phenomenon. One measure of the evolutionary success of apogamous species is the extent of their geographic range. This is particularly applicable in comparison with the ranges of closely related sexual species. Apogamy is reported in six of the 15 species in section Pellaea and in four, the apogamous races have wide ranges in North America or in both North and South America. In two species the apogamous types have been distinguished as varieties and are far wider ranging than the sexual counterpart. Thus, on the basis of their more extensive distributions, four of the apogamous forms are more successful than related sexual ones. The distribution of *P. intermedia* is not extensive, but within it the apogamous race has a broader distribution than the sexual race. There are some collections of *P. intermedia* from the Chisos mountains in Texas, within the range of the apogamous type, bearing on a single leaf some sporangia with 32 well-developed spores and others with a larger number of undeveloped spores. In *P. andromedifolia* the apogamous race is disjunct and not as abundant

as the sexual one. This contrasts with the distributions shown in the other species in which the apogamous race predominates, and suggests the possibility of a different evolutionary history in *P. andromedifolia*.

SUMMARY

Comparisons were made of epidermal cell and spore size of sexual diploid and apogamous triploid forms in three closely related species of *Pellaea* in a study of the effect of apogamy on morphological characters. Comparisons were also made with sexual diploid and sexual tetraploid forms in another species and with other members of *Pellaea*. Size of stomatal guard cells of the apogamous triploid plants relative to the sexual diploids in each of the species, was greater than would be expected on the basis of the chromosome levels alone. The same effect was not evident in comparisons of spores. In these cells the large size of the apogamous triploids relative to the sexual diploids was of the order that would be expected from the different chromosome levels.

Comparisons of the geographic distribution patterns of the sexual and apogamous races and with those of other members of the genus show that the apogamous types are wider ranging. However, in *P. andromedifolia* apogamous plants have a disjunct distribution and are not as abundant as the sexual ones.

The evolutionary potential of apogamous plants is shown in their production of functional antherozoids, their adaptation to different ecological niches, and their broad distributions. In these pellaeas differences in the ranges of the apogamous and sexual types are interpreted here as reflecting the dynamics of these reproductive systems in natural populations.

CHROMOSOME NUMBERS OF PELLAEA

Species	Locality and Collection	Mode of reproduction	Meiotic chromosome numbers	Ploidy
P. andromedifolia (Kaulf.) Fée	San Gabriel Mts. California *Karen Alt 3* — Fig. 1a	Sexual	29	2X
	Humboldt Co. California *S. Harris 21651* — Fig. 1b	Apogamous	87	3X
	Humboldt Co. *R. M. & A. F. Tryon 5557*	Sexual	29	2X
	Humboldt Co. *R. M. & A. F. Tryon 5556*	Apogamous	87	3X
	Point Mugu, Ventura Co., California *L. Kiefer 1132* — Fig. 1c	Apogamous	87	3X
P. intermedia Mett. ex Kuhn	Saltillo, Mexico *R. C. Rollins & R. M. Tryon 58144* — Fig. 1d	Sexual	29 (from 2n = 58)	2X
	Chiricahua Mts. Arizona *R. M. & A. F. Tryon 5089* — Fig. 1e	Apogamous	87	3X
P. ovata (Desv.) Weatherby	Gillespie Co., Texas *R. M. & A. F. Tryon 5029* — Fig. 1f	Sexual	29	2X
	San Luis Potosí, Mexico *R. C. Rollins & R. M. Tryon 58222* — Fig. 1g	Apogamous	87	3X
P. ternifolia (Cav.) Link var. *ternifolia*	Cuernavaca, Mexico *R. M. & A. F. Tryon 5105*	Sexual	29	2X
	San Luis Potosí, Mexico *R. C. Rollins & R. M. Tryon 58218*	Sexual	58	4X

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GRAY HERBARIUM, HARVARD UNIVERSITY

ON THE NAMES IN FRASER'S 1813 CATALOGUE

JAMES L. REVEAL

The 1813 Fraser's Catalogue (essentially accurately reprinted in Greene, 1890) and fully entitled "*A Catalogue of New and Interesting Plants, Collected in Upper Louisiana and Principally on the River Missourie, North America,*" which was published prior to August 1813, is known to nearly every botanist who has had the privilege of working with the names of Thomas Nuttall, the famous English taxonomist who made his greatest contributions in this country as a botanist, ornithologist, and explorer. This small document has been the source of controversy, neglect, and dispute for as many years as it has been in existence. Not only is its author questioned, its very nature as a place of publication for the species that appear in it is doubted by some.

Contrary to the beliefs of some, the author must have been Thomas Nuttall. The interested reader on this subject is invited to refer to the series of arguments presented by Shinners (1949, 1955, 1956) for Nuttall not being the author and the Catalogue as an invalid source of publication; Graustein's (1956) contentions that Nuttall was the author but that he considered the species not validly published because of an agreement with his sponsor, Benjamin Smith Barton of Philadelphia, not to publish any new species without Barton's consent; and Cronquist, Keck, and Maguire (1956) who believe that Nuttall was the author and that the Catalogue is a valid place of publication.

It has been common knowledge that Nuttall was at least associated with the names found in the Catalogue. Pennell (1936) and Graustein (1967) point out that he was in England and associated with the Fraser Brothers' Nursery at the time of publication. From Nuttall's two subsequent publications (1817, 1818) which followed shortly after the Catalogue, we know that he considered at least some of the

names as his own. Several of the early authors attributed the names in the Catalogue to Nuttall, and they certainly could have asked Nuttall if they had any doubt as who the author was. Pennell (1936) gives the impression that Nuttall was a rather shy and inhibited person. It would seem out of character for a man of such temperament to assume responsibility for the names in Fraser's Catalogue if he was not in any way responsible for them. It is inconceivable to me that someone else could have assigned names to Nuttall's own collection without Nuttall stating this fact later. If Nuttall was not associated with the entities, why should he later accept some of them as his unless he actually had given the names to the Fraser Brothers, helped someone who was employed by them to prepare the Catalogue, or perhaps have written the text himself. It should be noted here, however, that I do not say that Nuttall was the author of the paper, although Greene (1890) suggests this after seeing the copy of the Catalogue in Philadephia. What I do contend is that Nuttall is the author of the names in the paper, and thus, as provided by the International Code (1966), the species should be cited as "Nutt. in Fras."

Shinners (1956) goes to great length to show that several of the names in Fraser's Catalogue were not claimed by Nuttall in his later publications, and while this is true, I suspect that it was for reasons other than those given by Shinners. Some species were found to have been adequately described between 1813 and 1818 with names acceptable to Nuttall, but for those that were not, he used his own names that he had published in the Fraser's Catalogue. Nuttall occasionally cited only "Frasers Catalogue" and did not give himself credit for the name. Shinners uses this argument to show that Nuttall was not the author. The species with which I am most familiar that was published in the Catalogue is *Eriogonum flavum*. The name is credited to "Fras. Catal. 1813" and not starred as a new species in Nuttall's 1818 book, *The Genera of North American Plants*, and for this reason, Shinners suggested that Nuttall did not consider this species as his. Nothing is further from

the truth. In a detailed paper on this species in particular, and the genus *Eriogonum* in general, which Nuttall published in 1817, he makes a point of stating that he published the name *E. flavum* in Fraser's Catalogue. The reason why Nuttall simply stated "Fras. Catal. 1813." instead of "T. N. in Fras. Catal. 1813.", as he sometimes did, was probably to save space. To say that Nuttall was not the author of Fraser's Catalogue I believe is on more tenuous bases than to say that he was indeed the sole author. As no one else has come along to claim authorship of the species published in the list, this, I believe, proves the point that only Nuttall could have given the names to his own collection.

The International Code of Botanical Nomenclature (1966) states in Article 34 that "A name is not validly published . . . when it is not accepted by the author who published it . . ." As Nuttall did not specifically reject the names in the Catalogue, they must be considered as published. The arguments put forth by Graustein (1956) are immaterial. She states that under the terms of a contract, Nuttall's journals and observations became the exclusive property of Barton, and Nuttall was not supposed to do anything else but what was specifically stated in the contract. Thus, Graustein believes that Nuttall could not legally publish any new species in Fraser's Catalogue, for if he did, he would be breaking the terms of the contract. However, as McKelvey (1955) has pointed out, Nuttall's mere presence with the Overland Astorians as they ascended the Missouri River was breaking his contract with Barton, as was the shipping of his plants to England instead of Philadelphia. Certainly one more step in the breaking of the contract by publishing his findings would not be totally surprising.

Therefore, it is my desire in this paper to discuss each species listed in Fraser's 1813 Catalogue, basing the validity of the names on the adequacy of the descriptions and subsequent identifiability of each entity, considering the nomenclatural status and history of each, and making necessary adjustments and suggestions where necessary.

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1. *Allium reticulatum* Nutt. in Fras., nom. nud. This name was published in 1827 as *A. reticulatum* Nutt. ex G. Don in Wern., Nat. Hist. Soc. Mem. **6**: 36, but it was a homonym of *A. reticulatum* J. & C. Presl, Fl. Cech. 73. 1819. Nelson and Macbride later renamed this species *A. textile* in Bot. Gaz. **56**: 470. 1913.

2. *Allium stellatum* Nutt. in Fras., nom. nud. This species was a short time later described by Sims, referring to Nuttall's name in the Fraser's Catalogue, and should be cited as *A. stellatum* Nutt. ex Sims, Bot. Mag. **38**: pl. 1576. Aug. 1813.

3. *Alyssum petraeum* Nutt. in Fras., nom. nud. I have been unable to determine the identity of this nomen nudum. The name has not been treated by any subsequent author.

4. *Amorpha canescens* Nutt. in Fras., nom. nud. Pursh published this same name in Fl. Am. Sept. 2: 467. 1814, but made no reference to the Fraser's Catalogue.

5. *Amorpha nana* Nutt. in Fras. Catal. 1813. In my opinion this species is validly published in the Catalogue and should be accepted. Nuttall gives the following key points: ". . . elegant dwarf shrub, with highly odorous purple flowers . . . It is perfectly glabrous, dentures of the calyx all acuminate, and the legume one seeded." Pursh cites *A. nana* as a synonym of his own *A. microphylla* Pursh, Fl. Am. Sept. 2: 466. 1814.

6. *Astragalus crassicarpus* Nutt. in Fras. Catal. 1813. Barneby (1964) in his recent monograph on *Astragalus* succinctly states the problem on the Catalogue and this species as follows:

> "The status of the name *A. crassicarpus* is somewhat controversial, being vulnerable to criticism from two directions. The Fraser Brothers' Catalogue has been attacked and defended in recent years . . . as a valid medium of publication, neither side to the question having gained a conclusive victory. A graver fault is the extreme brevity of the original description and the fact that Nuttall himself [1818] adopted Pursh's *A. carnosus* in place of his own (or what is presumed to be his own) proposition. However no reasonable doubt has ever been entertained as to the identity of *A. crassicarpus,* which was already known to botanists contemporary with Nuttall."

The brief description noted by Barneby is just that: "Fruit about the size and form of *A. physodes,* but thick and succulent." Although it is brief, there is no question as to the species Nuttall had in mind. Pursh described *A. carnosus* in Fl. Am. Sept. 2: 740. 1814 from a Bradbury collection of *Sophora* (*S. nuttalliana* B. L. Turner) and fruits taken (according to Nuttall) from the Nuttall collection of *A. crassicarpus.* The species was later described as *A. caryo-*

carpus Ker in Bot. Reg. 2: 176, cum icone. 1816, from plants cultivated in Lambert's Garden from seeds that Nuttall had provided for the Fraser Brothers' Nursery.

7. *Astragalus melanocarpus* Nutt. in Fras., nom. nud. Nuttall apparently renamed this species *A. missouriensis* Nutt., Gen. N. Amer. Pl. 2: 99. 1818, but made no reference to the Fraser's Catalogue.

8. *Astragalus gracilis* Nutt. in Fras., nom. nud. Nuttall described this species in Gen. N. Amer. Pl. 2: 100. 1818, stating that his species ". . . appears to be *A. tenellus* of Pursh and also *Ervum multiflorum,* Suppl. 2. p. 739. It is likewise *Dalea parviflora* PH. 2. p. 474. as I have examined the specimen so marked in Herb. Lambert." As *A. tenellus* is a totally different species, Barneby (1964) comments: "Nuttall cited his own *A. gracilis* of Fraser's Catalogue, a nomen nudum, and *Dalea parviflora* Pursh . . . The name *A. gracilis* is therefore best treated as a legitimate substitute for *Dalea parviflora* . . ."

9. *Artemisia cernua* Nutt. in Fras., nom. nud. Nuttall described this species and ascribed the name in Fraser's Catalogue to himself in Gen. N. Amer. Pl. 2: 143. 1818, but by then Pursh had described the same species as *A. dracunculoides* Pursh, Fl. Am. Sept. 2: 742. 1814. When Pursh proposed his new species, he cited the name from Fraser's Catalogue, but as *A. nutans* instead of *A. cernua,* no doubt an error, in synonymy of his new species. It is generally agreed today that the American plant and the European one are conspecific and should be called *A. dracunculus* L.

10. *Aristida.* This grass genus is cited without a specific ephithet. Nuttall cites *A. pallens* Cav. in his Genera, but according to Hitchcock (1951), this is *A. oligantha* Michx. Possibly this is the grass cited.

11. *Batschia fimbriata* Nutt. in Fras., nom. nud. Pursh described this species as *B. longiflora* in Fl. Am. Sept. 1: 132. 1814, and Nuttall redescribed the species by the same name in Gen. N. Amer. Pl. **1:** 114. 1818, adding *B. decumbens.* In no instance is *B. fimbriata* referred to. The species is now known as *Lithospermum incisum* Lehm., Asperif. 303. 1818. The name *B. longiflora* is rejected because of *L. longiflorum* Salisb., 1796, while *B. decumbens* is rejected due to *L. decumbens* Vent., 1800.

12. *Bumelia confertiflora* Nutt. in Fras., nom. nud. This species is stated as having been collected near Saint Louis, Missouri. The only *Bumelia* found in that area is *B. lanuginosa* (Michx.) Pers. var. *oblongifolia* (Nutt.) R. B. Clark. Although Nuttall did not mention *B. confertiflora* when he described *B. oblongifolia* in Gen. N. Amer. Pl. 1: 135. 1818, it certainly must be the same plant. Neither Clark (1942) or Cronquist (1945) indicated the possible position of this nomen nudum.

13. *Bartonia decapetala* Pursh in Sims, Bot. Mag. **36:** pl. 1487. Aug. 1812. When Nuttall wrote the treatment for the Fraser's Catalogue, he indicated that this was a new species, and probably for him it was. Pursh apparently took notes from living material grown in England from seeds presented to the Fraser Brothers by Nuttall, and rushed into publication in Sims' Botanical Magazine the name of the new genus *Bartonia.* This action was probably not intended to beat Nuttall to the publication, but to please Benjamin Smith Barton, the teacher and sponsor of both Pursh and Nuttall. Needless to say, the name *Bartonia* had already been published by Muhlenberg for an entirely different plant. *Bartonia decapetala* later proved to belong to an already published genus, and is known now as *Mentzelia decapetala* (Pursh in Sims) Urban & Gilg, Ber. Deut. Bot. Ges. **10:** 263. 1892. A more detailed history of the feud between Nuttall and Pursh is given in McKelvey's book (1955).

14. *Bartonia polypetala* Nutt. in Fras., nom. nud., as *pollypetala*. This species name has not been treated by any subsequent author, but is probably the same plant later named *B. nuda* Pursh, Fl. Am. Sept. 1: 328. 1814. This species is now called *Mentzelia nuda* (Pursh) Torr. & Gray, Fl. N. Amer. **1**: 535. 1840.

15. *Chloris mucronata* Michx., Fl. Bor. Amer. 1: 59. 1803. This grass was included on the list in the Catalogue as one of the more interesting North American grasses available from the Fraser Brothers' Nursery. It is known presently as *Dactyloctenium aegyptium* (L.) Beauv.

15. *Chloris mucronata* Michx., Fl. Bor. Amer. 1: 59. 1803. 1803. Like the above grass, this one was cited in the Catalogue as being available from the Fraser Brothers' Nursery. It is known presently as *Bouteloua curtipendula* (Michx.) Torr.

17. *Cyperus*. An unspecified species of this genus was listed as available at the Fraser Brothers' Nursery. It was not indicated as being a new species.

18. *Cynoglossum glomeratum* Nutt. in Fras., nom nud. This species was described the following year by Pursh at which time he cited the Fraser Brothers' Catalogue as the source of his name. The citation should thus read: *C. glomeratum* Nutt. ex Pursh, Fl. Am. Sept. 2: 729. 1814. This species is now known as *Cryptantha celosioides* (Eastw.) Pays., Ann. Mo. Bot. Gard. **14**: 299. 1927.

19. *Calymenia nyctaginea* (Michx.) Nutt. in Fras. Catal. 1813, comb. nov. This new combination was later made in, and is usually dated from, Gen. N. Amer. Pl. 1: 26. 1818, by Nuttall. As there was no requirement in 1813 that a basionym be cited, the combination should be considered as made in the Catalogue. The species is now known as *Mirabilis nyctaginea* (Michx.) MacM.

20. *Calymenia pilosa* Nutt. in Fras., nom. nud. Nuttall in Gen. N. Amer. Pl. 1: 26. 1818 published this species, but by then Pursh had published *Allionia hirsuta* Pursh, Fl. Am. Sept. 2: 728. 1814, from a Bradbury collection. The species is presently known as *Mirabilis hirsuta* (Pursh) MacM.

21. *Calymenia angustifolia* Nutt. in Fras., nom. nud. Pursh cited this nomen nudum when he proposed *Allionia linearis* in Fl. Am. Sept. 2: 728. 1814, based on a Bradbury collection. Nuttall, in his Gen. N. Amer. Pl. 1: 26. 1818, described as new his *C angustifolia*, citing not only "T. Nuttall in Fraser's Catalogue. 1813." but the Pursh name as well. The species is now known as *Mirabilis linearis* (Pursh) Heimerl.

22. *Cactus viviparus* Nutt. in Fras. Catal. 1813. This species is certainly described here, although Nuttall redescribed it in Gen. N. Amer. Pl. 1: 295. 1818. The descriptive points given by Nuttall in 1813 are: "This species has much the appearance of *C. mamillaris*, but produces a large red flower, like *C. Flagelliformis*, and a greenish edible fruit, about the size of a grape." The species is now called *Coryphantha vivipara* (Nutt. in Fras.) Britt. & Brown, Ill. Fl. 2nd Ed. 2: 571. 1913. It should be noted that *Cactus mamillaris* of Nuttall is *Coryphantha missouriensis* (Sweet) Britt. & Rose.

23. *Cactus ferox* Nutt. in Fras., nom. nud. Nuttall later described this species in Gen. N. Amer. Pl. 1: 296. 1818, but was not aware that this name was a later homonym of *C. ferox* Willd., 1813. In 1828 de Candolle substituted *Opuntia missouriensis* DC., Prodr. 3: 472, for the Nuttallian species. The name *O. polyacantha* Haw., Syn Pl. Succ. Suppl. 82. 1819, however, was already available for the species.

24. *Cactus fragilis* Nutt. in Fras., nom. nud. As with the above species of cactus, Nuttall also described it in 1818, and this place of publication is the basis for *Opuntia fragilis* (Nutt.) Haw., Syn. Pl. Succ. Suppl. 82. 1819, the generally accepted name for this species.

25. *Cheiranthus asperus* Nutt. in Fras., nom. nud. Pursh did not attempt to ascertain the nature of this species in 1814, and thus this enabled Nuttall to describe the species as *C. asper* in Gen. N. Amer. Pl. 2: 69. 1818. This species is now called *Erysimum asperum* (Nutt.) DC., Syst. Veg. 2: 505. 1821.

26. *Cytisus rhombifolius* Nutt. in Fras., nom. nud. This species was described by Pursh in Fl. Am. Sept. 2: 741. 1814, at which time he cited the Fraser's Catalogue as the source of his name. Nuttall transferred the species from *Cytisus* to *Thermia* as *T. rhombifolia* (Nutt. ex Pursh) Nutt., citing both his name in the Catalogue and Pursh's place of publication. The species has since been transferred to *Thermopsis*, the citation being *T. rhombifolia* (Nutt. ex Pursh) Nutt. ex Richards. in Frankl. 1st. Journ. App. 737. 1823.

27. *Diodia virginica* L. This species was mentioned in the Catalogue as a plant that was available from the Fraser Brothers' Nursery.

28. *Dracocephalum cuspidatum* Nutt. in Fras. Catal. 1813. In my opinion the statement given "A Verticillate species" is enough to describe this species of mint. Nuttall later named this species as *D. parviflorum* Nutt., Gen. N. Amer. Pl. 2: 35. 1818, the name commonly used today. Of the species of *Dracocephalum* from the United States, as understood and known to Nuttall at that time, none but this has flowers that are verticillate, and this point is the first descriptive statement he used in describing *D. parviflorum*. The generic problem of whether or not to separate *Draco-*

cephalum and *Physostegia* is not for me to discuss, but if *D. cuspidatum* should be transferred to *Physostegia*, I can find no conflict.

29. *Dalea aurea* Nutt. in Fras., nom. nud. This species was described the following year by Pursh as *D. aurea* Nutt. ex Pursh, Fl. Am. Sept. 2: 740. 1814. Pursh based his description on a Bradbury collection, but cited the Fraser's Catalogue as the source of his name. Nuttall later redescribed this species using the same name in Gen. N. Amer. Pl. 2: 101. 1818, citing both the Fraser's Catalogue and Pursh's flora.

30. *Dalea enneandra* Nutt. in Fras. Catal. 1813. The description of this species is one of the more complete. Nuttall stated that the ". . . stem is tall and erect, sending out numerous slender waving branches towards its summit, terminated by racemes of white flowers, and silky calyces." Pursh renamed this species *D. laxiflora* in Fl. Am. Sept. 2: 741. 1814, and Nuttall accepted this name in his Gen. N. Amer. Pl. 2: 101. 1818, with no mention of his own species published five years before. It is difficult to determine whether Nuttall was rejecting his own name because of some taxonomic reason, or simply because the Pursh name seemed better. Nevertheless, Nuttall's name can not be rejected solely because Nuttall himself did not later accept it.

31. *Elaeagnus argentea* Nutt. in Fras., nom. nud., as *argenteus*. Pursh described this species under the same name in Fl. Am. Sept. 1: 114. 1814. As this name appeared in the first volume, I believe that Pursh was selecting the same name on the same basis as Nuttall selected the name. The name, however, is a homonyn of *E. argentea* Moench, Meth. Pl. 638. 1794 which is a superfluous substitute for *E. angustifolius* L., a different species entirely. The species is presently known as *E. commutata* Bernh. ex Rydb., Fl. Rocky Mts. 582. 1917. It should be noted that the citation

"*E. argentea* Colla, 1791," which is sometimes given as the earliest *E. argentea* is an error. Colla's name was published in Hort. Rip. in 1824.

32. *Evolvulus sessiliflorus* Nutt. in Fras., nom. nud. Pursh described this species as *Evolvulus argenteus* Pursh, Fl. Am. Sept. 1: 187. 1814, but made no reference to Fraser's Catalogue. This name, however, is a later homonym of *E. argenteus* R. Br., Prod. Fl. Nov. Holl. 489. 1810. Nuttall proposed a substitute name, *E. pilosus* in Gen. N. Amer. Pl. 1: 174. 1818, which is generally accepted as the valid name. Although *E. pilosus* was an alternative name which is now illegitimate under the Code, the rule is not retroactive. In no case is the nomen nudum mentioned.

33. *Echites puberula* Michx., Fl. Bor. Amer. 1: 120. 1803. This species was listed in the Catalogue as being available from the Fraser Brothers' Nursery. It is presently known as *Trachelospermum difforme* (Walt.) A. Gray.

34. *Eriogonum flavum* Nutt. in Fras. Catal. 1813. In my opinion this species is adequately described even though the only character given is "Fl. bright yellow." All of the other species in the genus known in 1813 had white flowers, and this note of distinction would certainly have held up if no other species were ever discovered. Pursh described this species as *E. sericeum* in Fl. Am. Sept. 1: 277. 1814, but the Nuttall name is commonly used.

35. *Erysimum montanum* Nutt. in Fras., nom. nud. I have been unable to discover what plant this nomen nudum is referable to. It has not been treated by any subsequent author.

36. *Ferula pubescens* Nutt. in Fras., nom. nud. This name was not adopted by Nuttall in 1818, as he named this plant *F. foeniculacea* Nutt., Gen. N. Amer. Pl. 1: 183. 1818. This species is now commonly called *Lomatium foeniculaceum*

(Nutt.) Coult. & Rose, Contr. U.S. Nat. Herb. 7: 222. 1900. In a recent revision of the species in this complex by Theobald (1966), the nomen nudum is not mentioned.

37. *Fritillaria americana* Nutt. in Fras., nom. nud. This species was described as *F. alba* Nutt., Gen. N. Amer. Pl. 1: 222. 1818, but with no reference to Fraser's Catalogue. The name *F. alba* is currently considered a nomen dubium. Beetle (1944) in her revision of the genus, states that the description is mainly that of a *Fritillaria*, and that the only species in the genus in the area where Nuttall visited is *F. atropurpurea* Nutt., Journ. Acad. Phil. 7: 54. 1834. Nevertheless, the description of the flowers states that they are "... rather large and white . . ." Ownbey (1940) suggests that this part of the description refers to *Calochortus nuttallii* Torr., which also occurs in the area that Nuttall collected in 1811. It might be well to comment in this connection that the flowers of *F. atropurpurea*, when poorly prepared, blacken as do several other white-flowered species, and it might have been that Nuttall simply forgot their true color. Until the type can be located, the name had best be considered a nomen dubium, but I feel that a case could be made to remove that title if it were seriously attempted.

38. *Gonolobus hirsutus* Michx., Fl. Bor. Amer. 1: 119. 1803. This species was listed as one of the interesting plants that could be obtained from the Fraser Brothers' Nursery. Donald J. Drapalik of the University of North Carolina, informs me that he believes this name, a new name for *Vincetoxicum acanthocarpus* Walt., is referable to *Matelea carolinensis* (Jacq.) Woodson.

39. *Gaura coccinea* Nutt. in Fras., nom. nud. The first place of valid publication for this species is *G. coccinea* Nutt. ex Pursh, Fl. Am. Sept. 2: 733. 1814, and the description is based on a Bradbury collection, but with the citation of the Catalogue as the source of the name.

40. *Hypericum surculosum* Nutt. in Fras., nom. nud. I have been unable to determine what species from along the Mississippi River this nomen nudum refers to.

41. *Hyssopus anethiodorus* Nutt. in Fras. Catal. 1813. When Nuttall described this species, he pointed out the unique feature of the flower color when he said "Both calyx and corolla blue," for at that time, only two other species were known from the United States. These species, *Agastache nepetoides* (L.) Kuntze with greenish-yellow flowers and *A. scrophulariifolium* Willd.) Kuntze with purplish flowers, were both well known to Nuttall. By pointing out the obviously distinguishing feature, the species, in my opinion, is validly published. Pursh described the same species as *Stachys foeniculum* Pursh, Fl. Am. Sept. 2: 407. 1814, and Nuttall redescribed the same species as *H. anisatus* in Gen. N. Amer. Pl. 2: 27. 1818, citing only the Pursh name in synonymy. Inasmuch as *H. anethiodorus* is validly described, the proper name should be *A. anethiodora* (Nutt. in Fras.) Britt. in Britt. & Brown, Ill. Fl. 3: 85. 1898.

42. *Jussieua angulata* Nutt. in Fras., nom. nud. This species was described as *J. leptocarpa* Nutt., Gen. N. Amer. Pl. 1: 299. 1818, but with no reference to the name in Fraser's Catalogue. This species is currently called *Ludwigia leptocarpa* (Nutt.) Hara, Jour. Jap. Bot. 28: 292. 1953.

43. *Linum perenne* L. var. *americanum* Nutt. in Fras., nom. nud. This same plant was named *L. lewisii* Pursh, Fl. Am. Sept. 1: 210. 1814, but by the time Nuttall wrote his treatment of the genus for his flora, he considered that the differences between the American and European plants were not great enough to warrant even varietal separation. Since then, however, the trend has been to recognize the American phase as *L. perenne* L. ssp. *lewisii* (Pursh) Hult.[1]

[1]Like many American taxonomists, I have been slow in accepting the reality that *L. lewisii* was not as distinct from *L. perenne* as one should prefer distinct species to be. By having an opportunity to study

44. *Lilium andinum* Nutt. in Fras. Catal. 1813. In my opinion the description given by Nuttall is adequate enough to determine what species of lily he had in mind, and thus the name should be considered as validly published. He states that this species ". . . has affinity to *L. Catesboei*, but the stem is usually 3-5 flowered." The following year, Pursh published *L. umbellatum* in Fl. Am. Sept. 1: 229. 1814, citing only a Nuttall specimen but making no reference to Fraser's Catalogue. When Nuttall republished *L. andinum* in Gen. N. Amer. Pl. 1: 221. 1818, he cites his name from the Catalogue.

The species is closely related to *L. philadelphicum* L., and should be considered as a variety, var. *andinum* (Nutt.) Ker., Bot. Reg. 7: pl. 594. 1821. Wherry (1947) states that the combination proposed by Ker-Gawler was of subspecific rank, but as one may see, Ker-Gawler distinctly says that his new combination was at the varietal rank when he wrote: "We have thought it safer to keep the two [i.e. *L. philadelphicum* and *L. andinum*] under the same specific title, assorting to each its particular synoymy below the head of its variety."

45. *Liquiritia lepidota* Nutt. in Fras., nom. nud. This name was first published in Pursh, and may be cited as *Glycyrrhiza lepidota* Nutt. ex Pursh, Fl. Am. Sept. 2: 480. 1814. When Nuttall redescribed this species in Gen. N. Amer. Pl. 2: 106. 1818, he stated why he no longer used the name *Liquiritia* when he said: "This plant appears to destroy the

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herbarium material in the major herbaria across the United States during my Internship at the U.S. National Herbarium, I came to realize that Hultén's treatment of our plant was most acceptable. This means, however, that a rare, high alpine ecotype of this species from Nevada must have its nomenclature adjusted, and is to be now known as **L. perenne** ssp. **lewisii** var. **saxosum** (Maguire & Holmgren) Reveal, comb. nov., based on *L. lewisii* var. *saxosum* Maguire & Holmgren, Leafl. West. Bot. 4: 265. 1946. During the summer of 1964, Noel H. Holmgren, of the New York Botanical Garden, and I found a single specimen of this variety on top of Mt. Jefferson in the Toquima Mountains, Nye Co., Nevada. This extended the known range of this variety south from its type locality in the Ruby Mountains.

artificial distinctions by which *Glycyrrhiza* and *Liquiritia* have been separated; as it can be equally referred to either one or the other."

46. *Lathyrus myrtifolius* Muhl. in Willd., Sp. Pl. 3: 1091. 1803. This plant is listed in the Catalogue as available from the Fraser Brothers' Nursery.

47. *Lactuca oblongifolia* Nutt. in Fras. Catal. 1813. In considering the species of *Lactuca* that Nuttall was familiar with from the United States, and the plants which Nuttall considered to belong to this genus, all had yellowish flowers. Therefore, his characterization of his new species as having "Fl. blue." is, in my opinion, a valid description. Within the related genus *Sonchus*, there are several blue-flowered species including some from Missouri, but as Nuttall placed them in *Sonchus*, this does not in any way invalidate the Nuttall species published in the Catalogue. Although these blue-flowered species of *Sonchus* have subsequently been transferred to *Lactuca*, Nuttall did not, at that time, consider them to be members of the genus *Lactuca*.

The following year, Pursh described *Sonchus pulchellus* in Fl. Am. Sept. 2: 502. 1814. Later, Nuttall decided to rename both as *L. integrifolia* in Gen. N. Amer. Pl. 2: 124. 1818, at which time he cites his name from the Catalogue, and Pursh's 1814 species. Thus, as *L. oblongifolia* was a validly and properly described species, it should replace *L. pulchella* (Pursh) DC., Prodr. 7: 134. 1838, which is presently the commonly used name for this species.

48. *Liatris graminifolia* (Walt.) Willd., Sp. Pl. 3: 1636. 1803. This species was listed as one of the more interesting species that could be obtained from the Fraser Brothers' Nursery.

49. *Liatris paniculata* Willd., Sp. Pl. 3: 1637. 1803. This was listed as one of the more interesting species that could

be obtained from the Fraser Brothers' Nursery. Its exact identity, however, was questioned.

50. *Mentzelia oligosperma* Nutt. in Fras., nom. nud. This nomen nudum was first published by Sims as *M. oligosperma* Nutt. ex Sims, Bot. Mag. **42**: pl. 1760. 1815, citing Fraser's Catalogue as the source for his name. It is interesting to note that while the Catalogue was not signed, or in any way credited directly to Thomas Nuttall who by 1815 had not in print credited himself with any of the names in the Catalogue, Sims had no question as to who the author of this species was.

51. *Malva coccinea* Nutt. in Fras. Catal. 1813. Nuttall describes this species as follows: "Flowers scarlet, produced in dense spikes," a sufficient description to consider Fraser's Catalogue as the original place of publication. Pursh made the combination *Cristaria coccinea* in Fl. Am. Sept. 2: 453. 1814, citing "Malva coccinea, *Fraser. catal.*" This species was again described by Nuttall in Gen. N. Amer. Pl. 2: 81. 1818, at which time he cited his original description and indirectly referred to Pursh's new combination. He states rather briskly that "This plant has no sort of affinity to *Cristaria,* and by the fruit is a genuine Malva." In considering the Catalogue as the place of publication, typification of the species must be changed from the Lewis collection cited by Pursh to the Nuttall collection. This species is currently known as *Sphaeralcea coccinea* (Nutt. in Fras.) Rydb., Bull. Torr. Bot. Club **40**: 58. 1913.

52. *Oenoplea volubilis* (Linn. f.) Nutt. in Fras., comb. nov., as *Oenoplia.* This new combination is based on *Rhamnus volubilis* Linn. f., Suppl. 152. 1781. The combination here was made before that of Roemer & Schultes who proposed the same combination in Syst. Veg. 5: 332. 1819. The species is now known as *Berchemia scandens* (Hill) K. Koch, Dendrol. **1**: 602. 1869. This latter combination might be noted as it is usually attributed to Trel., Trans. Saint

Louis Acad. 5: 364. 1889. The species was listed as one of the more interesting plants that could be obtained from the Fraser Brothers' Nursery.

53. *Oenothera cespitosa* Nutt. in Fras. Catal. 1813. This species is amply described by Nuttall when he states that "This species is more perfectly stemless than *Oe. acaulis*, of Cavanilles, from which it is perfectly distinct. Flowers very large and white, with dilated obcordate petals." Pursh described the same species from a Lewis collection as *Oe. scapigera* in Fl. Am. Sept. 1: 263. 1814, but as the species is adequately described in the Catalogue, it should be cited as the original place of publication.

54. *Oenothera albicaulis* Nutt. in Fras., nom nud. When Pursh described *Oe. albicaulis* in Fl. Am. Sept. 2: 734. 1814, he cited the Fraser's Catalogue as the source of his name, but did not have the same Evening Primrose in mind that Nuttall had when he proposed the name. As the Nuttall name in the Catalogue is a nomen nudum, the citation of the Pursh species must be given as *Oe. albicaulis* Pursh without any reference to the Catalogue. Nuttall later redescribed his *Oe. albicaulis* from his material in Gen. N. Amer. Pl. 1: 245. 1818, and pointed out the error that Pursh had made in associating his species with that of Nuttall's. As the Nuttall name was a later homonym, we refer to his distinct species as *Oe. nuttallii* Sweet, Hort. Brit. ed. 2, 199. 1830.

55. *Oenothera serrulata* Nutt. in Fras., nom. nud. This species was later described without reference to the Catalogue as *Oe. serrulata* Nutt., Gen. N. Amer. Pl. 1: 246. 1818.

56. *Oenothera macrocarpa* Nutt. in Fras. Catal. 1813. Although Nuttall adequately described this species there has been a reluctancy to take up the name because of the more commonly used name *Oe. missouriensis* Sims, Bot. Mag.

39: pl. 1592. Nov. 1813. Nuttall described the species as follows: "The fruit of this species readily distinguishes it from every other, being remarkably compressed, and furnished with four broad wings." It is my opinion that Pursh was not describing as new *Oe. macrocarpa* in Fl. Am. Sept. 2: 734. 1814, as generally assumed, but was giving the Nuttall name to the plant that had been adequately described, and putting the Sims name in synonymy. It seems certain that Pursh was taking his name from Fraser's Catalogue even though it is not cited. The name "*macrocarpa*" is not one that one would just happen to come up with.

When Nuttall wrote his Genera in 1818, he proposed an entirely different name for this species, *Oe. alata* Nutt., Gen. N. Amer. Pl. 1: 248. He cited "*Oe. macrocarpa* Ph" as a synonym, but as the name in the Catalogue was validly published, it can not be discarded, even by its author.

In accepting this name, which has been recently accepted in Gleason & Cronquist (1963), the following new combinations are proposed following the recent treatment of the family by Munz (1965):

Oe. macrocarpa Nutt. in Fras. var. **incana** (A. Gray) Reveal, comb. nov., based on *Oe. missouriensis* Sims var. *incana* A. Gray, Bost. Jour. Nat. Hist. **6**: 189. 1850.

Oe. macrocarpa Nutt. in Fras. var. **oklahomensis** (J. B. S. Norton) Reveal, comb. nov., based on *Megapterium oklahomense* J. B. S. Norton, Rep. Missouri Bot. Gard. **9**: 153. 1898.

57. *Orobus diffusus* Nutt. in Fras., nom. nud. I have been unable to determine the exact identity of this nomen nudum. It is probably the same as *O. dispar* Nutt., Gen. N. Amer. Pl. 2: 95. 1818, which is a synonym of *Astralagus tenellus* Pursh, Fl. Am. Sept. 2: 473. 1814. This species is often diffuse. Index Kewensis (Jackson, 1895) says that the nomen nudum is referable to *Vicia americana* Muhl. ex. Willd., Sp. Pl. 3: 1096. 1802, but Hermann (1960) makes no mention of this name in his revision of the genus.

58. *Oxytropis acuminata* Nutt. in Fras., nom. nud. As Barneby (1952) points out, this nomen nudum must be referable to *O. lambertii* Pursh, Fl. Am. Sept. 2: 740. 1814. The species was described with no reference to Fraser's Catalogue. Nuttall accepted the Pursh name without comment.

59. *Phalangium esculentum* Nutt. in Fras. Catal. 1813. Nuttall based this name on two elements which are now separated as distinct species. Both species have blue flowers, the character used by Nuttall to distinguish it from the other yellow-flowered species in the United States. The fact that we know he had in mind both species can be seen both in the original description in which he states that "The roots of this plant is eaten by the Savages of the Missourie and Columbia Rivers," and later in his Genera in which he discusses the wide distribution of the single species as he conceived it.

The element of the species that Nuttall himself collected was illustrated by Sims, and a new combination proposed, as *Scilla esculenta* (Nutt. in Fras.) Sims, Bot. Mag. 38: pl. 1574. Aug. 1813.[1] This illustration was made from plants grown in the Fraser Brothers' garden from seeds collected, according to Nuttall (1818), near the Huron River and also from around Saint Louis.

The following year, Pursh described the second element of the Nuttall species, and I doubt that Nuttall ever saw this plant before 1813. Lewis had collected *P. quamash* Pursh in Fl. Am. Sept. 1: 226. 1814, from Clearwater Co., Idaho (Gould, 1942), and this was the plant Nuttall referred to in his comments about the Columbia River Indians who used the root for food. This information probably came to Nuttall from the fur traders and trappers that he was travelling with in 1811. The Columbia River plant was later collected by David Douglas, and from cultivated plants grown in England, *Camassia esculenta* Lindl., Bot. Reg. 18: pl.

[1]On the basis of this reference, the Catalogue is considered to have been published prior to August, 1813.

1486. 1832, was described and Lindley placed *P. quamash* in synonymy under his own new species. Lindley was explicit in stating that his *C. esculenta* was not *P. esculenta* of Nuttall or *S. esculenta* Sims, even though he was using the same specific name "*esculenta*" for his new species.

Gould (1942) handles the nomenclature properly, calling the eastern species that Nuttall had originally named *P. esculentum*, *Camassia scilloides* (Raf.) Cory, Rhodora 38: 405. 1936. He called the western species which Pursh had named *P. quamash* and later renamed *C. esculenta* by Lindley, *C. quamash* (Pursh) Greene, Man. Bot. Bay Reg. 313. 1894.

60. *Podalyria mollis* Michx., Fl. Bor. Amer. 1: 264. 1803. This species is questionably identified in the Fraser Catalogue. It must have been the same plant that Nuttall later described as *Baptisia leucophaea* in Gen. N. Amer. Pl. 1: 282. 1818, which Nuttall stated was collected near Saint Louis. *Podalyria mollis* is now known as *Thermopsis mollis* (Michx.) M. A. Curtis ex A. Gray.

61. *Potentilla mollis* Nutt. in Fras., nom. nud. I have been unable to determine the identity of this nomen nudum as it is not mentioned by Pursh or Nuttall. Nor has it been treated in either of the two Rydberg revisions of the genus (1898, 1908). I suspect that it may possibly be the same as *P. humifusa* Nutt., Gen. N. Amer. Pl. 1: 310. 1818, not Willd., 1813, which is now known as *P. concinna* Richards. in Frankl. 1st. Journ. 739. 1823, since that was the only new *Potentilla* described by Nuttall.

62. *Pycnanthemum dichotomum* Nutt. in Fras., nom nud. It has been impossible to determine exactly what species of *Pycanthemum* Nuttall had in mind when he proposed this name. He described two new species in his Genera, and of these two, he apparently collected only *P. pilosum* Nutt. himself. This species, published in Gen. N. Amer. Pl. 2: 33. 1818, was grown at the Fraser Brothers' Nursery, and the nomen nudum may be referred to this species.

63. *Penstemon angustifolium* Nutt. in Fras., nom. nud., as *Pentstemon.* This species was subsequently published as *P. angustifolium* Nutt. ex Pursh, Fl. Am. Sept. 2: 738. 1814, at which time Pursh cites the Fraser Catalogue as the basis for his name. Nuttall chose to reject this name stating that he could not refrain from adopting *P. caeruleum* Nutt., Gen. N. Amer. Pl. 2: 52. 1818, over *P. angustifolium* ". . . which I had formerly given . ." The species is now called *P. angustifolium.*

64. *Penstemon grandiflorum* Nutt. in Fras. Catal. 1813. I am inclined to consider this species as published and that the comments given by Nuttall are distinctive enough to make an unquestionable recognition of this species. Nuttall states: "Flower about the size and form of *Digitalis purpurea,* and spontaneously subject to great variation in color." Later, under *P. erianthera,* Nuttall comments: "*P. grandiflorum* is nearly the commonest species in that country, and it was first met with near the confluence of the river Platte, from whence it continues to the Andes, frequently occurring in vast fields, together with the *scarlet mallow,* which form a brilliant object, visible at some miles distance."

Of the known species of *Penstemon* in 1813, this was certainly the only large flowered species, and the similarity of the flower to *Digitalis* is apparent. Pursh described the same species as *P. bradburii* Pursh, Fl. Am. Sept. 2: 738. 1814, and this species name would have to be adopted if the Nuttall name should be deemed invalid.

65. *Penstemon cristatum* Nutt. in Fras., nom. nud. Nuttall described this species as *P. cristatum* in Gen. N. Amer. Pl. 2: 52. 1818, but by that time, Pursh had described the species as *P. erianthera* Pursh, Fl. Am. Sept. 2: 737. 1814. In attempting to apply the Nuttall name *P. erianthera,* Pursh mistakenly applied the name to the plant that Nuttall had called *P. cristatum.* Therefore, the name of this species must be *P. erianthera* Pursh.

66. *Penstemon teretiflorum* Nutt. in Fras., nom. nud. Nuttall described this species as *P. albidum* in Gen. N. Amer. Pl. 2: 53. 1818, citing his nomen nudum as a synonym.

67. *Penstemon erianthera* Nutt. in Fras., nom. nud. As noted above, under *P. cristatum*, Pursh misapplied the Nuttall name to that species, and the plant that Nuttall had called *P. erianthera*, Pursh proposed *P. glaber* in Fl. Am. Sept. 2: 738. 1814. When Nuttall described his *P. erianthera* in Gen. N. Amer. Pl. 2: 52. 1818, he placed the Pursh name in synonymy in an attempt to correct the Pursh error. However, the rules of nomenclature do not allow such superfluous substitutes, and this species must be called *P. glaber* Pursh.

68. *Passiflora lutea* L. This species was listed as one of the more interesting plants which was available at the Fraser Brothers' Nursery.

69. *Petalostemon violaceum* Michx., Fl. Bor. Amer. 2: 50. 1803. This species was listed as an interesting plant which was available at Fraser Brothers' Nursery. The correct name for this species is *Dalea purpurea* Vent., Hort. Cels. pl. 40. 1800.

70. *Petalostemon candidum* (Willd.) Michx., Fl. Bor. Amer. 2: 49. 1803. This species was listed as an interesting plant which was available at the Fraser Brothers' Nursery. The correct name for this species is *Dalea candida* Willd., Sp. Pl. 3: 1337. 1802.

71. *Psoralea macrorhiza* Nutt. in Fras., nom. nud. Pursh described this species, naming it *P. cuspidata* Pursh, Fl. Am. Sept. 2: 741. 1814, and cited the Nuttall nomen nudum in synonymy. The Pursh name was accepted by Nuttall in his Genera without comment.

72. *Psoralea esculenta* Nutt. in Fras., nom. nud. Pursh published this species as *P. esculenta* in Fl. Am. Sept. 2: 475.

1814, without reference to the Fraser Catalogue. Nuttall later, in Gen. N. Amer. Pl. 2: 102. 1818, credited himself with the name from Fraser's Catalogue, and put the Pursh citation in synonymy.

73. *Psoralea incana* Nutt. in Fras., nom. nud. Pursh described this species as *P. argophylla* in Fl. Am. Sept. 2: 475. 1814, the name this species may be known as today. Later, Nuttall published his name *P. incana* in Gen. N. Amer. Pl. 2: 102. 1818, and placed the Pursh name in synonymy.

74. *Ribes longiflorum* Nutt. in Fras., nom nud. According to Torrey & Gray, Fl. N. Amer. 1: 552. 1840, this species is *R. aureum* Pursh, Fl. Am. Sept. 1: 164. 1814. In 1834, Nuttall claimed authorship of this name when he cited Wyeth's collection of *Ribes aureum*. Nuttall wrote: "Ribes *longiflorum*, Nuttall, in Fraser's Catalogue, 1813. So named one year previous to Pursh's publication."

75. *Rudbeckia columnifera* Nutt. in Fras. Catal. 1813. In my opinion, this species is adequately described in Fraser's Catalogue, as Nuttall states:

> "Spontaneous varieties of this plant sometimes occur with bright fulvous flowers, coloured like *Tagetes patula:* the stem is simple, seldom producing more than three flowers, which are of an uncommon length, appearing like a column of flosculi, subtended by 5-8 neutral florets, and a simple calyx."

This species was also described as *R. columnaris* Sims, Bot. Mag. **39**: 1601. 1813, from cultivated plants given to Sims by the Fraser Brothers who had grown the species from seeds collected by Nuttall. The Pursh name, *R. columnaris* Pursh, Fl. Am. Sept. 2: 575. 1814, is an illegitimate substitute for Nuttall's *R. columnifera*, and is thus an exact synonym of it. The species is now commonly known as *Ratibida columnifera* (Nutt. in Fras.) Woot. & Standl., Contr. U.S. Nat. Herb. **19**: 706. 1915.

76. *Rudbeckia purpurea* L. var. *serotina* Nutt. in Fras. Catal. 1813. In my opinion, this variety is validly published. Nuttall redescribed this variety in Gen. N. Amer. Pl. 2: 178. 1818, but with no reference to Fraser's Catalogue. In the Catalogue, the descriptive comments are: "Stem somewhat branching and hirsute, fls. brighter and more numerous." This form is usually referred to *Echinacea purpurea* (L.) Moench.

77. *Saccharum brevibarbe* (Michx.) Pers., Syn. Pl. 1: 103. 1805. This species was listed in the Catalogue as one of the interesting plants that could be obtained from the Fraser Brothers' Nursery. It is now known as *Erianthus brevibarbis* Michx., Fl. Bor. Amer. 1: 55. 1803.

78. *Seseli lucidum* Nutt. in Fras., nom. nud. This name was never published, and Nuttall mentions it as a synonym under *S. divaricatum* Pursh, Fl. Am. Sept. 2: 732. 1814. According to Mathias & Constance (1944), the nomen nudum is referable to *Musineon divaricatum* (Pursh) Nutt. ex Torr. & Gray var. *hookeri* Torr. & Gray.

79. *Stylosanthes racemosa* Nutt. in Fras., nom. nud. I have been unable to determine the identity of this nomen nudum.

80. *Sideranthus integrifolius* Nutt. in Fras., nom. nud. The name *Sideranthus* was proposed as a new genus, but as it lacks a description, it was not validly published. It was not until 1840 that Nuttall finally accepted the name as his. The identity of this species has not been definitely ascertained. Pursh, on the basis of a Bradbury specimen, placed *S. integrifolius* under his *Amellus villosus* in the Addenda et Corrigenda section of the Flora on page 750. Steudel, Nom. 775. 1821, also places *S. integrifolius* under *A. villosus*. The Steudel publication is often cited as the first place to indicate what the Nuttall nomen nudum refered to.

81. *Sideranthus pinnatifidus* Nutt. in Fras., nom. nud. This name was referred to *Amellus spinulosus* Pursh, Fl. Am. Sept. 2: 750. 1814, an opinion in which Hall (1928) concurs under *Haplopappus spinulosus* (Pursh) DC., Prodr. 5: 347. 1836.

82. *Sycios angulata.* The genus name *Sycios* is an alternate spelling for *Sicyos.* The Fraser Brothers were offering for sale *Sicyos angulatus* L. through their Nursery.

83. *Troximon ciliatum* Nutt. in Fras., nom. nud. Pursh published this species as *T. cuspidatum* in Fl. Am. Sept. 2: 742. 1814. Later, Nuttall described *T. marginatum* in Gen. N. Amer. Pl. 2: 128. 1818, citing the Pursh species in synonymy. The species is now known as *Microseris cuspidata* (Pursh) Schultz-Bip., Pollichia 22-24: 309. 1866.

84. *Troximon glaucum* Nutt. in Fras., nom. nud. This species was described as *T. glaucum* Pursh, Fl. Am. Sept. 2: 505. 1814, but with no reference to Fraser's Catalogue. Index Kewensis (Jackson, 1895) indicates that the name should be cited as Nutt. ex Pursh. The plant is now called *Agoseris glauca* (Pursh) Raf., Herb. Raf. in Extra of Atl. Journ. 6: 39. 1833.

85. *Thuraria herbacea* Nutt. in Fras., nom. subnud. Cronquist (1957) stated that in his opinion this species is a *nomen dubium,* and this opinion he still holds. In corresponding with Dr. Cronquist on this species, he has written: "Neither *Gutierrezia* nor *Euthamia* can be excluded on the basis of the original publication alone, although one might have a good suspicion that the plant would turn out to be a *Grindelia.* The point is that a good suspicion is not enough. When it is not clear that the author is even trying to provide a botanical description, then his comments must make the application of the name unmistakably plain if the name is to be considered validly published."

The species was described as having "Fl. yellow, and the calyx resiniferous." Nuttall also stated that the species occurred in open ground along the Missouri River. Dr. Alfred E. Schuyler of the Academy of Natural Sciences in Philadelphia has informed me that there is a collection of this species in the Academy Herbarium, but under the name *Donia squarrosa*. Pursh described *D. squarrosa* in Fl. Am. Sept. 2: 559. 1814, which Nuttall later accepted in his Genera without comment or reference to the name published in Fraser's Catalogue.

Although I feel certain that Nuttall had *Grindelia squarrosa* (Pursh) Dunal, Mém. Mus. Par. 5: 50. 1819, in mind when he proposed his new genus *Thuraria*, he did not adequately separate it from related genera, and thus it can not be considered as validly published.

86. *Uniola latifolia* Michx., Fl. Bor. Amer. 1: 70. 1803. This plant was listed as one of the interesting new grasses that was available at the Fraser Brothers Nursery.

87. *Virgilia grandiflora* Nutt. in Fras. Catal. 1813. Nuttall described this species as follows: "This fine species differs essentially from *V. bicolor*, in being perennial, and producing a simple stem, terminated by one to three large flowers: its entire pappus also distinguishes it from *V. fimbriata*." Pursh published this species as *Gaillardia aristata* Pursh, Fl. Am. Sept. 2: 573. 1814, thinking the plant to be an annual on the basis of the Lewis collection. On page 570, Pursh cites *V. grandiflora* from the Catalogue, and corrects his error, indicating that the species is perennial.

Shinners (1956) stated that if *V. grandiflora* is considered as validly published, then a new combination would be necessary. Cronquist (1957) however, pointed out that there is already a *Gaillardia grandiflora* Hort. ex Lemaire, Ill. Hort. 4: pl. 139. 1857, and thus the proper name for our plant is still *G. aristata* Pursh.

88. *Vitis campestris* Nutt. in Fras., nom. subnud. The only descriptive term used in the statement given by Nuttall is

"bushy," and it is my opinion that this does not validly distinguish this species from *V. riparia* Michx., Fl. Bor. Amer. 2: 231. 1803. The Nuttall name is referable to the Michaux species.

89. *Yucca glauca* Nutt. in Fras. Catal. 1813. Nuttall adequately described this species which was later named *Y. angustifolia* Pursh, Fl. Am. Sept. 1: 227. 1814. Later, however, "Nuttall did not take up his own name, but chose that of Pursh, and made no reference to the earlier name in Fraser's Catalogue. The original description is: "Leaves narrow, and filiferous; capsule dry, coriaceous, and large as that of *Y. gloriosa*."

DEPARTMENT OF BOTANY
BRIGHAM YOUNG UNIVERSITY
PROVO, UTAH 84601

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A CYTOTAXONOMIC STUDY OF THE HERBACEOUS SPECIES OF SMILAX: SECTION COPROSMANTHUS*

Jose K. Mangaly

The herbaceous species of *Smilax* (section *Coprosmanthus*), widely distributed both in the Old and the New World, have their greatest concentration in the eastern half of the United States. The genus has been conventionally placed in the family Liliaceae. Ventenat isolated it from the Liliaceae and placed it under Smilaceae. Rafinesque removed the herbaceous species from *Smilax* on the basis of their non-prickly stems and the presence of staminodes in pistillate flowers, and placed them under a new genus *Nemexia*. Later, Torrey relegated these taxa to a new section, *Coprosmanthus* within the genus *Smilax*. Kunth, in turn, raised section *Coprosmanthus* to the level of genus. The naturalness of the new genus has often been questioned and most recent authors refer to the herbaceous species

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Voucher specimens and slides are deposited in the herbarium of The Catholic University of America.

under a section of *Smilax*. Small retained the genus name *Nemexia* in his Flora of the Southeastern United States and recognized eight species. Pennell, in his revision of the herbaceous species of *Smilax*, recognised nine species. Fernald, in Gray's Manual Ed. 8, and Gleason in Manual of Vascular Plants, recognised only three species and two varieties.

Thus, there is a diversity of views as to the number of species within this section and as to the circumscription of species and varieties. In many of the herbaria checked, misapplied names are often the rule rather than the exception. Moreover, no cytological work has been done within these taxa except for *Smilax herbacea*. The necessity of a revision is thus apparent.

The present study is an attempt to bring together all available information in order to clarify existing problems, especially at the specific level, with the hope that this synthesis may help to illuminate sectional relationships. Breeding experiments were not performed since seeds failed to germinate in culture. Acquaintances with local and regional populations, their habitats, and variability have been of extreme importance to the study.

Chromosomal information has been proved to be a significant aid, especially in elucidating the matter of dioecism in these taxa. Except for one taxon, chromosome numbers are uniform throughout section *Coprosmanthus*. I feel that many of the problems existing in this complex have been solved by this attempt.

The genus *Smilax* was proposed by Tournefort and later was included in Systema Naturae (1735) by Linnaeus. The genus included dioecious plants with flowers composed of six perianth parts, six stamens (more than six in the section *Pleiosmilax*), superior ovary of three carpels and 1-2 ovules in each locule.

Rafinesque (1825) circumscribed the herbaceous species with perennial rhizomes and annual herbaceous, non-prickly aerial shoots in a new genus, *Nemexia*. Torrey (1843) classified *Smilax herbacea (S. peduncularis, S. pulverulenta*

and *S. lasioneuron* were recognised as synonyms of *S. herbacea)* under the section *Coprosmanthus*, omitting the two other binomials, *S. pseudo-china* and *S. tamnifolia*, already published at that time. Kunth (1850) raised the section *Coprosmanthus* to the level of genus. De Candolle (1878) divided the genus *Smilax* into four sections, *Nemexia*, *Eusmilax*, *Coilanthus*, and *Pleiosmilax*, these being mainly based on the number of ovules, nature of perianth at anthesis and number of stamens. *Nemexia* was characterized by recurved perianth, six stamens, and biovulate carpels. However, *S. china* and its relatives, with woody stems and uniovulate carpels, were relegated to the section *Nemexia*. Koyama (1960) suggested that de Candolle included *S. china* under the section *Nemexia* thinking that the section is characterized by a single ovule to a locule but, in fact, de Candolle mentioned the biovulate locule in his description of the section: *"Flores musculi hexandri, sepalis petalisque plus minus excurvatis; feminei loculis biovulatis . . ."*

Most European authors, e.g., Bentham and Hooker (1883) and Krause (1930), followed de Candolle's system. However, most American authors have recognised two sections, *Eusmilax* and *Nemexia*, for the North American species. These sections generally divide the woody from the herbaceous taxa. Koyama (1960) divided *Smilax* (world wide basis) into six sections, *Pleiosmilax*, *Smilax*, *Macranthae*, *Coilanthus*, *China* and *Coprosmanthus*. The section *Coprosmanthus* is based mainly on the somewhat reflexed nature of the tepals at anthesis, presence of staminodes in pistillate flowers, and the fact that the petioles and blades fall off together. By rules of priority, *Coprosmanthus* is to be retained for the section that includes all the herbaceous species in the United States.

Linnaeus (1753) recognised two herbaceous species, *S. herbacea* and *S. pseudo-china*, from the North American Continent. Michaux (1803) added two more species, *S. pulverulenta* and *S. tamnifolia*. In the present paper, *S. tamnifolia* is recognised as a synonym of *S. pseudo-china*. Hooker (1840) added another species *S. lasioneuron*. Engel-

mann (1835) recognised a new variety, *S. herbacea* var. *ecirrhata*. However, the new varietal epithet was first validly published by Kunth (1850) as *Coprosmanthus herbaceous* var. *ecirratus*. Gray (1848) recognized two species and one variety in the section *Coprosmanthus;* Watson (1890) raised the variety *S. herbacea* var. *ecirrhata* to the rank of species in the 6th ed. of Gray's Manual.

Small (1898) circumscribed two new species, *S. tenuis* and *S. diversifolia*, but later (1903) he re-established the genus name *Nemexia* for the herbaceous species *Smilax* and recognised two more species, *N. hugeri* and *N. biltmoreana*. The taxonomic position of *S. tenuis* is not clear. Even though the stem and leaves are slender, it resembles *S. lasioneuron* in many respects and representative specimens are extremely rare in most herbaria checked. In the present treatment, *S. diversifolia* is included within *S. lasioneuron*. Pennell (1910) described a new variety, *S. herbacea* var. *crispifolia*, based on its relatively thick leaves, a character common among plants of this species growing in direct sunlight; in the present treatment, *S. herbacea* var. *crispifolia* is considered as an ecological variant. Pennell in 1916 attempted a taxonomic revision of the section and added one more species, *S. leptanthera*. This also, in the present treatment, is regarded as an ecological variant. Ahles (Radford, et. al. 1964) reduced *S. hugeri* and *S. biltmoreana* to two varieties of *S. ecirrhata*.

The section *Coprosmanthus* has a wide distribution on the eastern half of the North American Continent extending from the Gulf area to the Lake region and northward into Canada. In all eight species recognized, the annual shoots develop very early in the spring. Flower buds are already developed by the time the shoots emerge from the soil. The flowering period generally lasts about two weeks for each species; however, there is considerable variation within and between species with regard to the time of flowering. Most species flower between early May and late June. Therefore, a major part of the field work was done during these months

in 1963, 1964 and 1965. Representative specimens and cytological material were collected from Florida, South Carolina, North Carolina, Virginia, Maryland, Pennsylvania, Michigan, Illinois, and Wisconsin.

Most of the materials for cytological studies (especially flower buds) were collected in the field. The most favorable time of fixation was found to be between 11:30 A.M. and 12:30 P.M. Materials collected at other times showed practically no mitotic stages. In a few cases, however, good meiotic stages were obtained from flower buds collected early in the morning. Attempts were made to transplant rhizomes to the greenhouse. Shoots were cut back and the rhizomes were dug out and transplanted in pots and then transported to the greenhouse. Most specimens of *S. ecirrhata* complex, all with short erect shoots, survived while most specimens of *S. herbacea* complex, all with long climbing shoots, died in the greenhouse.

More than 20 random population samples of *Smilax herbacea* were collected from Virginia, Maryland, and Pennsylvania. A few population samples of *S. lasioneuron* and *S. pulverulenta* were also obtained. *Smilax hugeri, S. biltmoreana,* and *S. pseudo-china* were represented by widely spaced individuals rather than by populations. Therefore, only single specimens of these species could be acquired. Measurements were made mostly on herbarium specimens. Care was taken to select the specimens from wide geographic ranges. The list of herbaria consulted is provided elsewhere.

CHROMOSOMAL STUDIES

Because of the high morphological and ecological variability and wide distribution of the members of this section, it was thought early in the study that chromosomal information might be of considerable value in dealing with taxonomic problems. It soon became apparent that the number $n = 13$ was constant for nearly all members of the section, the exception being *S. pseudo-china.*

Methods:

Root tip and flower bud squashes were used for chromosomal studies. Both materials were pre-treated with 0.002 mol/L solution of 8-hydroxyquinoline (ortho) and were fixed in modified Carnoy's fixative (4 chloroform: 3 absolute ethanol: 1 glacial acetic acid). The materials were kept in Carnoy's fixative for 24 hours and then preserved in 70% ethanol or were used immediately after thorough washing. Initial use of aceto-orcein and aceto-carmine procedures was abandoned since the meristematic cells became highly refractory and because certain granular bodies became as heavily stained as chromosomes.

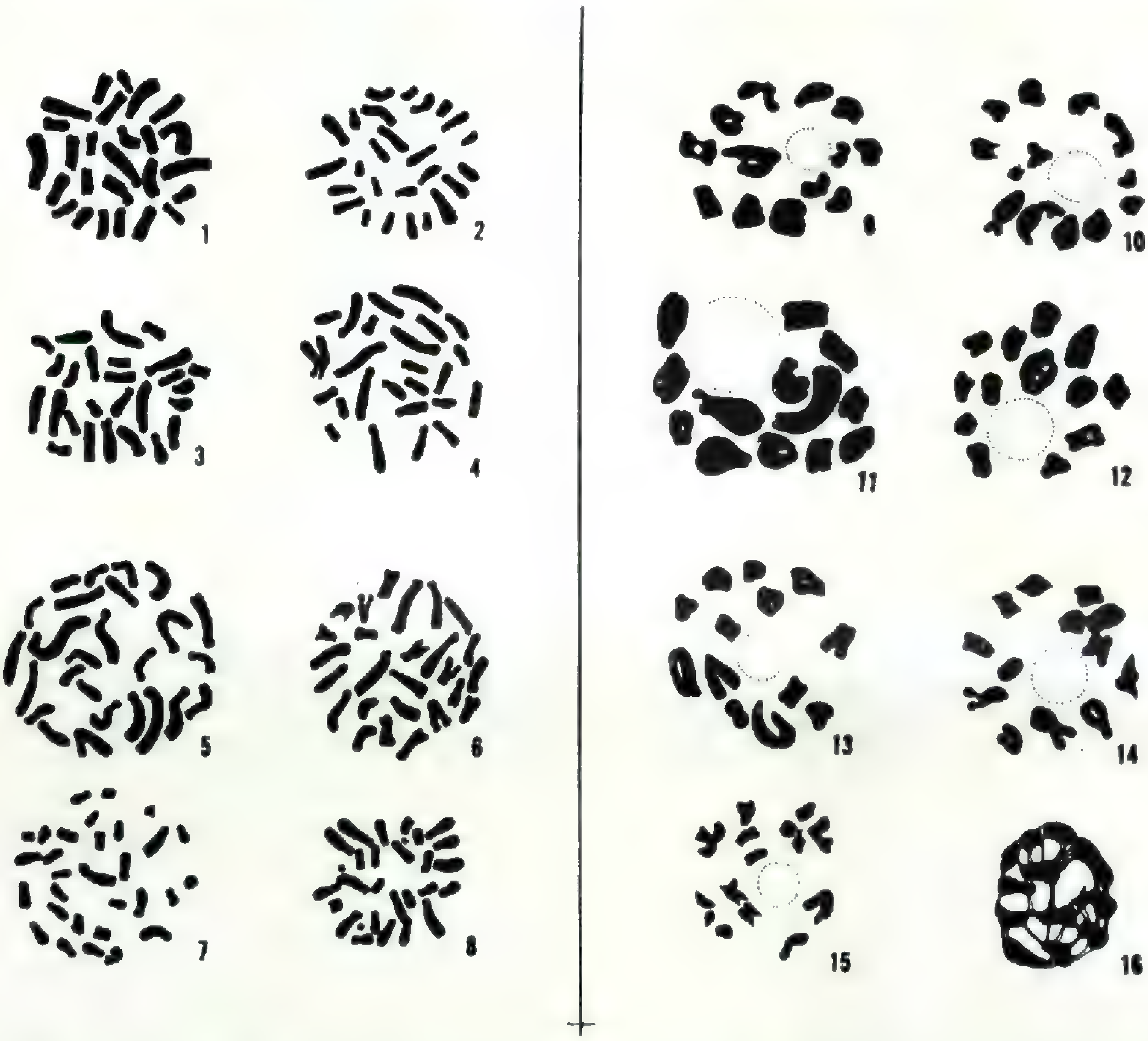
A satisfactory staining procedure resulted from modifying Marimuthu and Subramaniam's (1960) hematoxylin squash technique. Both flower buds and root tips were hydrolysed in a mixture of concentrated HCl and absolute ethyl alcohol (1:1) for about one minute, then washed thoroughly in distilled water and mordanted in 2% ferric ammonium sulphate for about 5-10 minutes. The material was then washed in distilled water and stained in a time-ripened solution of hematoxylin for 10-15 minutes. (Other materials may require a longer staining period; overstaining is seldom a serious problem.) The tissue was softened and destained in 45% acetic acid at 60°C. for about one minute. Both hydrolysing and destaining time depend on the size and texture of the material. The material was then mounted in a drop of the same solution of 45% acetic acid and squashed under the coverslip. A quick survey of these temporary mounts was made, and good preparations were made permanent, using the CO_2 freeze technique, and mounted in green euparal. The chromosomes were stained dark blue with the background almost colorless.

Drawings were made with the aid of a camera lucida. In some cases chromosomes were respaced to avoid overlapping.

Results:

Only one previous chromosomal count was reported for this section, *S. herbacea*, $n = 13$ (Lindsay 1930). In the

following list, counts are recorded for plants of all 8 species comprising *Coprosmanthus.* All plants of the 8 species except those of *S. pseudo-china* have chromosome numbers $2n = 26$ (Figs. 1-6 and 9-14). Two specimens of *S. pseudo-china,* both from South Carolina, have a chromosome number $2n = 30$ (Figs. 7 and 15). Within karyotypes, chromosomes exhibit great variability with regard to their size and morphology. The longest chromosomes measure 6 microns



Figs. 1-8. Mitotic chromosomes of *Smilax* species. — 1. *S. lasioneuron.* — 2. *S. herbacea.* — 3. *S. illinoensis.* — 4. *S. pulverulenta.* — 5. *S. hugeri.* — 6. *S. biltmoreana.* — 7. *S. pseudo-china.* — 8. an apparent hybrid of *S. biltmoreana* and *S. hugeri,* showing the extra chromosome fragments.

Figs. 9-16. Meiotic chromosomes of *Smilax* species. — 9. *S. Lasioneuron* — 10. *S. herbacea.* — 11. *S. illinoensis.* — 12. *S. pulverulenta.* — 13. *S. hugeri.* — 14. *S. biltmoreana.* — 15. *S. pseudo-china.* — 16. an apparent hybrid of *S. biltmoreana* and *S. hugeri* showing the lateral pairing of the bivalents.

while the shortest, 2 microns and there is gradation between these two extremes (Fig. 17). In all taxa, all chromosomes display subterminal centromeres. *S. pseudo-china* appears to have the smallest and *S. illinoensis* has the largest.

The plants of the genus *Smilax* are dioecious. Lindsay (1930) made an extensive study of the chromosomes of *S. herbacea* and reported the absence of any heteromorphic pair. On the other hand, she noticed at the periphery of the spindle an unusual pair of chromosomes with near terminal centromeres and practically free ends. From her figures, this chromosome pair appears to be one of the largest within the karyotype. She also suggested that the folding of the free end of a chromosome might result in the members of the pair appearing unequal in length. Such a case can only be verified when both the chromosomes of a homologous pair are seen in the profile view.

An attempt was made to determine the chromosomal basis of sex differentiation in this section. Microsporocytes of *Smilax* species here investigated disclose the presence of a

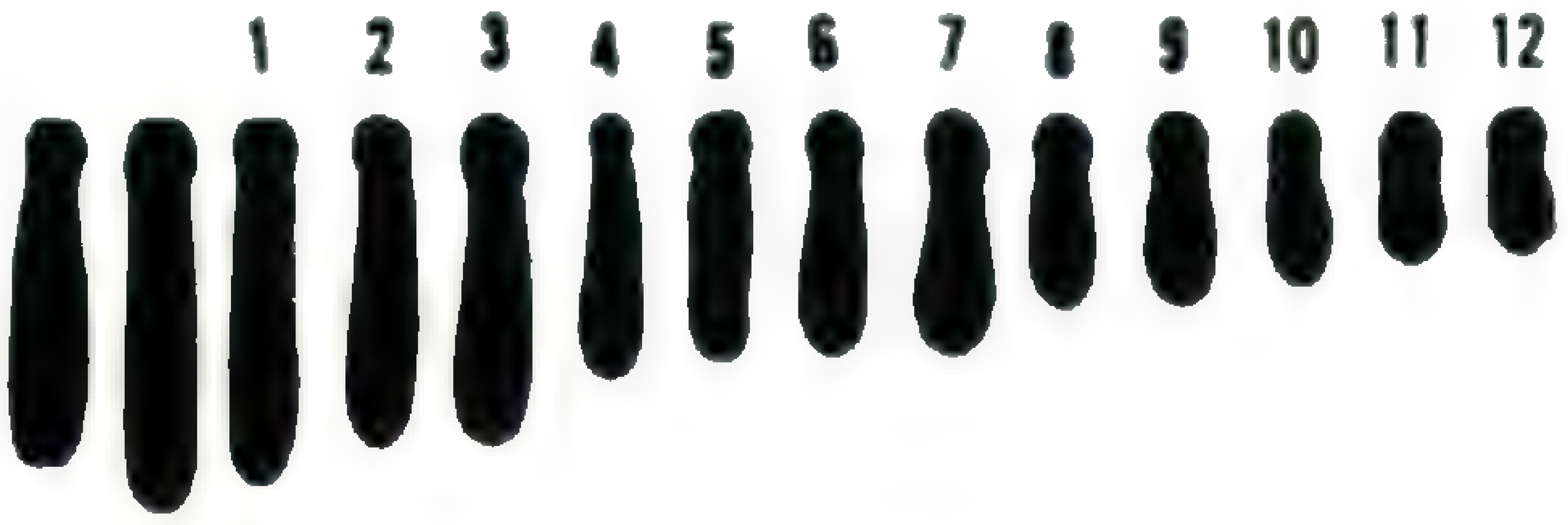


Fig. 17. Karyotype of *S. pulverulenta*. 1-12 somatic chromosomes, and the other two apparently sex chromosomes.

pair of unequal chromosomes during synapsis. This pair, one of the largest within the karyotype, is fairly distinct up to diakinesis (Figs. 9, 11, 12, and 13). Even at this stage the difference in size of the two chromosomes is not very prominent, and gradually it becomes indistinct during late prophase and metaphase as the chromosomes become further contracted. It is likely that this pair of unequal chromosomes with long free arms is the same that Lindsay observed in the periphery of the spindle. The presence of this heteromorphic pair during synapsis in microsporocytes suggests the possibility that the sex differentiation in *Smilax*, section

Coprosmanthus, is by X and Y chromosomes, where XX is female and XY is male. Such distinct heteromorphic pairs are noticed only in four species where very good stages of early prophase of the 1st meiotic divisions were obtained. In all other species this could not be verified. Therefore, at the present time this observation is far from conclusive.

Two specimens with perfect flowers were found in the herbarium materials checked. Both specimens were collected from Wisconsin. Attempts to collect bisexual living materials from their original localities were not successful. Therefore, no cytological investigation could be made.

CHROMOSOME NUMBERS

Taxon	*Coll. No.*	*County*	*Source*	n *PMC*	2n *Mitosis*
Smilax herbacea			VIRGINIA		
	219		1.5 mi. south of Lewis Mt., Shenandoah National Park	—	26
	2135		Lewis Mountain, Shenandoah National Park . .	13	26
	2137		4 mi. south of Lewis Mt., Shenandoah National Park	13	—
	2136		4 mi. south of Lewis Mt., Shenandoah National Park	13	—
			PENNSYLVANIA		
	2002	Lycoming	Williamsport, Pa. . .	—	26
	2073	Clearfield	2 mi. south of Coal Hill on Route 219, Pa. . .	—	26
S. lasioneuron			MICHIGAN		
	2145	Washtenaw	East of Delhi Rd., Delhi	—	26
			ILLINOIS		
	2146	Cook	2 mi. west of Roselle on Route 72	—	26
	2147	Cook	2 mi. west of Roselle on Route 72	13	26
	2148	Cook	2 mi. west of Roselle on Route 72	—	26

Taxon	*Coll. No.*	*County*	*Source*	n *PMC*	2n *Mitosis*
			WISCONSIN		
	2152	Iowa	Jct. Rt. 18 and K, 1 mi. on K.	—	26
	2154	Iowa	Jct. Rt. 18 and K, 1 mi. on K.	—	26
	2163	Iowa	On Route 23 . .	—	26
	2166	Iowa	Jct. Rt. 23 and Rt. 14	13	—
	2167	Iowa	Jct. Rt. 23 and Rt. 14	13	26
	2168	Iowa	Jct. Rt. 23 and Rt. 14	13	26
	2170	Iowa	Jct. Rt. 23 and Rt. 14	—	26
S. pulverulenta			VIRGINIA		
	206	Bath	Doutat State Park	—	26
	210	Allegheny	Strom, between Covington and Eagle Rock . .	—	26
			MARYLAND		
	231	Montgomery	Cabin John Park . .	—	26
	2123	Montgomery	Cabin John Park . .	13	26
	2124	Prince Georges	Laurel, Rt. 1, 15 mi. north of D.C. . .	—	26
	2126	Prince Georges	Laurel, Rt. 1, 15 mi. north of D.C. . .	13	26
	2127	Prince Georges	Laurel, Rt. 1, 15 mi. north of D.C. . .	—	26
S. pseudo-china			SOUTH CAROLINA		
	270	Sumter	6.8 mi. s.w. of Sumter on Route 15 . .	—	30
	275	Orangeburg	2 mi. from Jct. Rt. 176 and 15, on Route 176 . .	15	30
S. illinoensis			MICHIGAN		
	2143	Washtenaw	E. Delhi Road, Delhi . .	13	26
	2144	Washtenaw	E. Delhi Road, Delhi . .	—	26
S. hugeri			FLORIDA		
	282	Jackson	Marianna Caverns, Fla.	13	26

Taxon	*Coll. No.*	*County*	*Source*	n *PMC*	2n *tosis Mi-*
	285	Jackson	Marianna Caverns, Fla.	13	26
	291	Jackson	Marianna Caverns, Fla.	—	26
S. biltmoreana			FLORIDA		
	281	Jackson	Marianna Caverns, Fla.	13	—
	290	Jackson	Marianna Caverns, Fla.	—	26
	283	Jackson	Marianna Caverns, Fla.	—	26
S. ecirrhata			WISCONSIN		
	2180	Iowa	Jct. Rt. 23 and Rt. 14	—	26

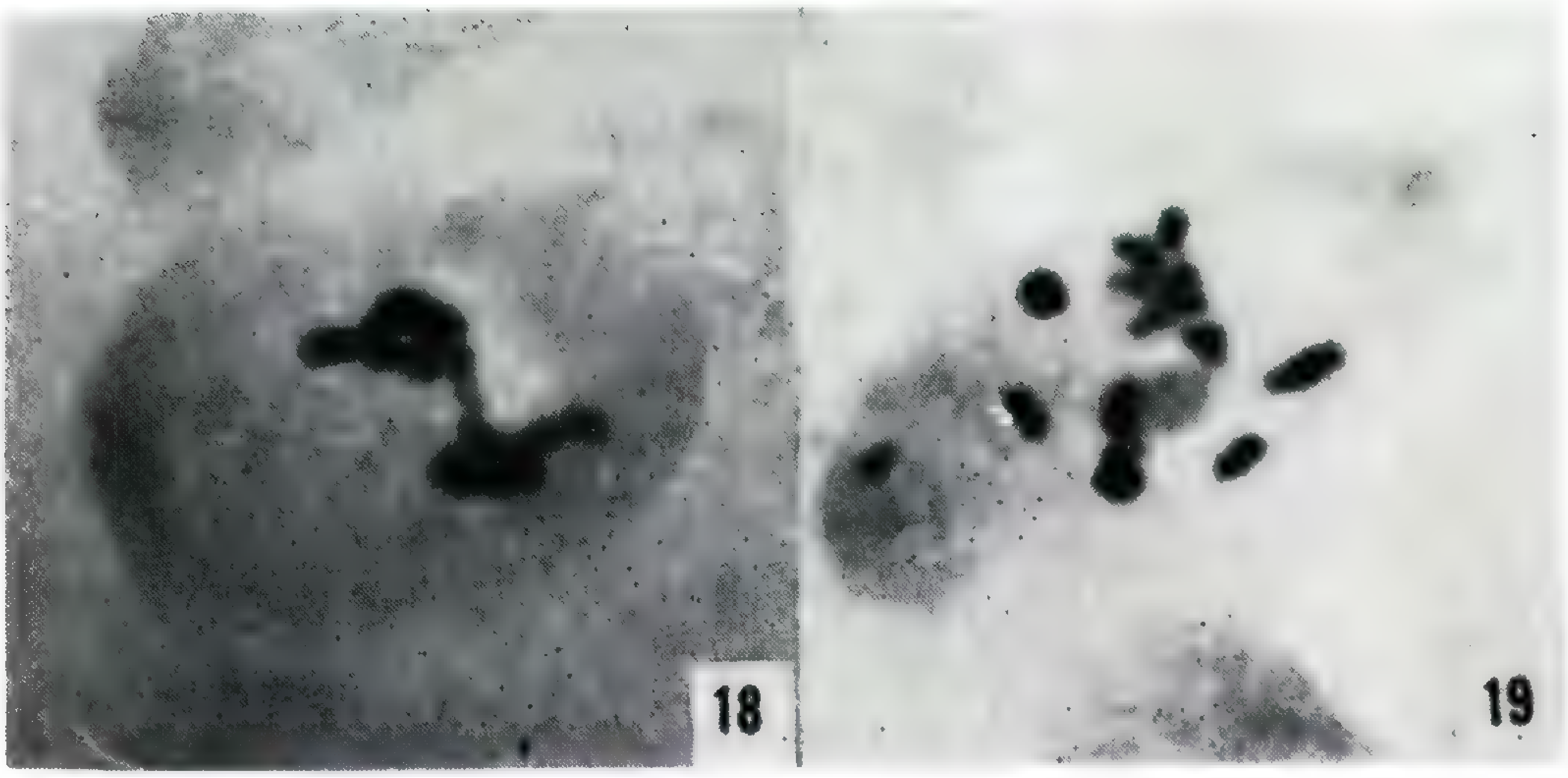
CHROMOSOMAL ABERRATIONS IN THE SMILAX BILTMOREANA-S. HUGERI COMPLEX

Exomorphologically intermediate forms of *Smilax biltmoreana* (Small) J. B. Norton and *S. hugeri* (Small) J. B. Norton are collected from undisturbed mixed woodland habitats near Marianna, Florida. Careful examination of herbarium specimens of these species indicates that populations from certain other localities are similarly confusing taxonomically. In these cases, misapplied names are the rule rather than the exception. This morphological evidence has suggested interspecific hybridization as a working hypothesis.

A total of fourteen plants from the Marianna population collected in the spring of 1964 was examined cytologically. Root tip and flower bud squashes were used for chromosomal studies. Both materials were fixed and stained as described previously. Nine of these were morphologically typical of the species. These plants exhibited a diploid chromosome-number of 26, and meiotic behavior was normal for the approximately 150 PMCs examined. However, three of the remaining five intermediate forms exhibited extra-chromosome fragments varying from two to eight, in addition to the normal chromosome complement (Fig. 8).

Abnormal meiotic pairing is conspicuous in intermediate forms. The synapsed chromosomes show lateral connections

Plate 1372.



Figs. 18 and 19. Photomicrographs of pollen mother cells of *Smilax hugeri* — *S. biltmoreana* hybrids showing the unusual synaptic configurations. 18. thirteen bivalents in two small rings connected together. 19. the bivalents becoming free — six pairs still interconnected. (1200 ×).

between adjacent bivalents and without exception are arranged in rings or chains (Figs. 16, 18, and 19). Usually ten pairs form an outer ring with the other three remaining inside, interconnected. In most cells examined the later stages of meiotic divisions were apparently normal. Occasionally, however, lagging chromosomes were observed in anaphase. In anaphase I, the bivalents disengage and then continue normal anaphasic separation.

Examination of pollen under the microscope indicated that 35% of the pollen was shrivelled up in these plants which showed the cytological ring formation. Attempts were made to test pollen germination. Incubation at room temperature in 3% sucrose resulted in pollen tube formation in only 17% of 1000 grains examined.

The observed chromosomal aberrations in *Smilax* hybrids differ from the translocation systems in *Oenothera* and in *Rheo* by the presence of bivalent rings and chains. Although the available data are insufficient for a conclusive appraisal of the process they suggest that these aberrations result from a large number of reciprocal translocations of very

small units. Sterility of hybrids due to structural hybridity involving small chromosomal segments was suggested by Sax as early as 1933, for *Campsis chinensis* × *C. radicans*, and a large number of cases are known where hybrids show complete or partial sterility. The suggestion of Stebbins (1950) on the origin of translocations in connection with cryptic structural hybridity seems appropriate for *Smilax*. Equally important is the fact that when a translocation results in a deficiency in one chromosome, it also results in a duplication in another chromosome. If the chromosome complements of the hybrid parents have more translocated duplications than deletions it is likely that these hybrids might show more of structural aberrations at synapsis and less of sterility. (A manuscript with details of these observations has been submitted for publication.)

A few cytological problems remain unsolved. Two bisexual individuals collected from Wisconsin were found among the herbarium specimens. Attempts to collect such specimens in the spring of 1965 for cytological studies were not successful.

All species of this section except *S. pseudo-china* produce only one peduncle from a node. But some specimens of *S. pseudo-china*, especially from South Carolina and coastal Virginia, have three peduncles at the same node, a central long one and two shorter lateral ones. Whether there is a cytological basis for this atypical expression has not been determined.

MORPHOLOGIC AND TAXONOMIC CRITERIA

It is very difficult to evaluate morphological characters which are used taxonomically in this section, as most features are extremely variable in relation to ecological and climatic variations. This is particularly true in the case of the *S. herbacea* complex where the relative length of the peduncle and the leaf vary on the same plant. Also there is considerable variation in leaf shape between young and older plants. Consequently, taxonomic distinctions are mainly based on a combination of morphological features.

The characters listed below are useful principally in the determination of specific categories.

Habit. *Smilax ecirrhata* and associates are all small erect plants with no tendrils or with a few rudimentary ones. *Smilax illinoensis,* an intermediate form between *S. lasioneuron* and *S. ecirrhata*, is also erect and has a large number of tendrils mostly on the upper part of the stem. All others are fairly tall and climbing. All have perennial rhizomes with a few strong fibrous roots. The juvenile stage lasts about 3 - 6 years. Shoots from mature rhizomes of the *S. herbacea* complex often produce a few branches. Among older plants, more than one shoot usually appear from the same rhizome in one season.

Leaves. The shape of the leaf, number of veins, presence or absence of pubescence, character of tip and base, relative length of petiole and blade were used to differentiate species. The floral characters in this group are evolutionarily conservative and, therefore, vegetative characters like the morphology of the leaf have been used in delineating species even though such characters are ecologically plastic.

Leaf shape varies not only on different individuals of the same species, but on the same plant, depending on its location on the plant, and also among plants of different age. So extreme care should be taken to define species, with emphasis on the leaf shape. Another significant feature in the case of plants of the *S. herbacea* complex is that on older plants there is a gradual transition from scaly bracts at the base of the stem to the normal foliage leaves above. Pubescence and non-pubescence on the under-surface of the leaves of different species appear to be fairly constant. Of the three species with non-pubescent leaves, two grow mostly at higher elevations along the Appalachian Mountains and the third is restricted to the eastern Coastal Plain. Species with pubescent leaves extend to higher elevations too. This is especially true of *S. lasioneuron* which is dis-

tributed mostly in the central plains but is also found in the Great Smoky Mountain region and the eastern part of the Rockies.

Inflorescence. The inflorescence is a few to many flowered umbel. Its place of origin, whether axillary to bracts or not, is considered as an important taxonomic character for separation of species. The number of umbels and the number of flowers on each peduncle are also useful.

Perianth. The shape and the relative length and breadth of tepals are useful. In general, the inner ones are progressively narrower. Often the pistillate flowers have smaller tepals. In all species the tepals are light green and free.

Stamens. In most species the ratio of length of filament to that of another is not uniform within the same flower, the outer ones with longer filaments and the inner ones slightly shorter. In general, however, relative length of anthers and filaments was found to be useful. In most species the anthers are shorter than the filaments; only in one are the anthers longer. These features are reliable only if the flowers are fully open.

Fruits. The fruit is a one-seeded to six-seeded berry. It is relatively uniform in shape, but color varies from blue to black among different species. The fruit wall is either glaucous or not. The number of seeds in a berry does not appear to be a species character even though the short *S. ecirrhata* complex has fewer seeds per fruit.

Branching. Only in the *S. herbacea* complex is branching prevalent and here the pattern of branching is almost the same in all species. Branches usually develop on the upper half of the stem. The leaves on the branches in general are smaller than those on the mature stem and vary more in shape. Thus, for most taxonomic purposes, only leaves on the stem were considered.

FLOWERING

Preliminary investigations suggested that flowering in this section is not photoperiodically controlled. In early spring, when the annual shoots sprout, the flower buds develop along with them, even before the leaves fully expand. Thus, flowering begins before the shoot is exposed to any photoperiodic influence. As expected, the southern forms of a given species flower slightly earlier than the northern ones.

Smilax hugeri is the earliest to flower, beginning in early April and reaching its peak in the third week of April. *Smilax pseudo-china*, occurring sympatrically with *S. hugeri* in the Carolinas, reaches its peak flowering in May. *Smilax biltmoreana*, which occurs mostly in the mountains, has its peak flowering period during the second and third weeks of May. *Smilax pulverulenta* reaches its peak flowering in the second week of May and *S. lasioneuron*, with a farther northward distribution, has a peak flowering period from

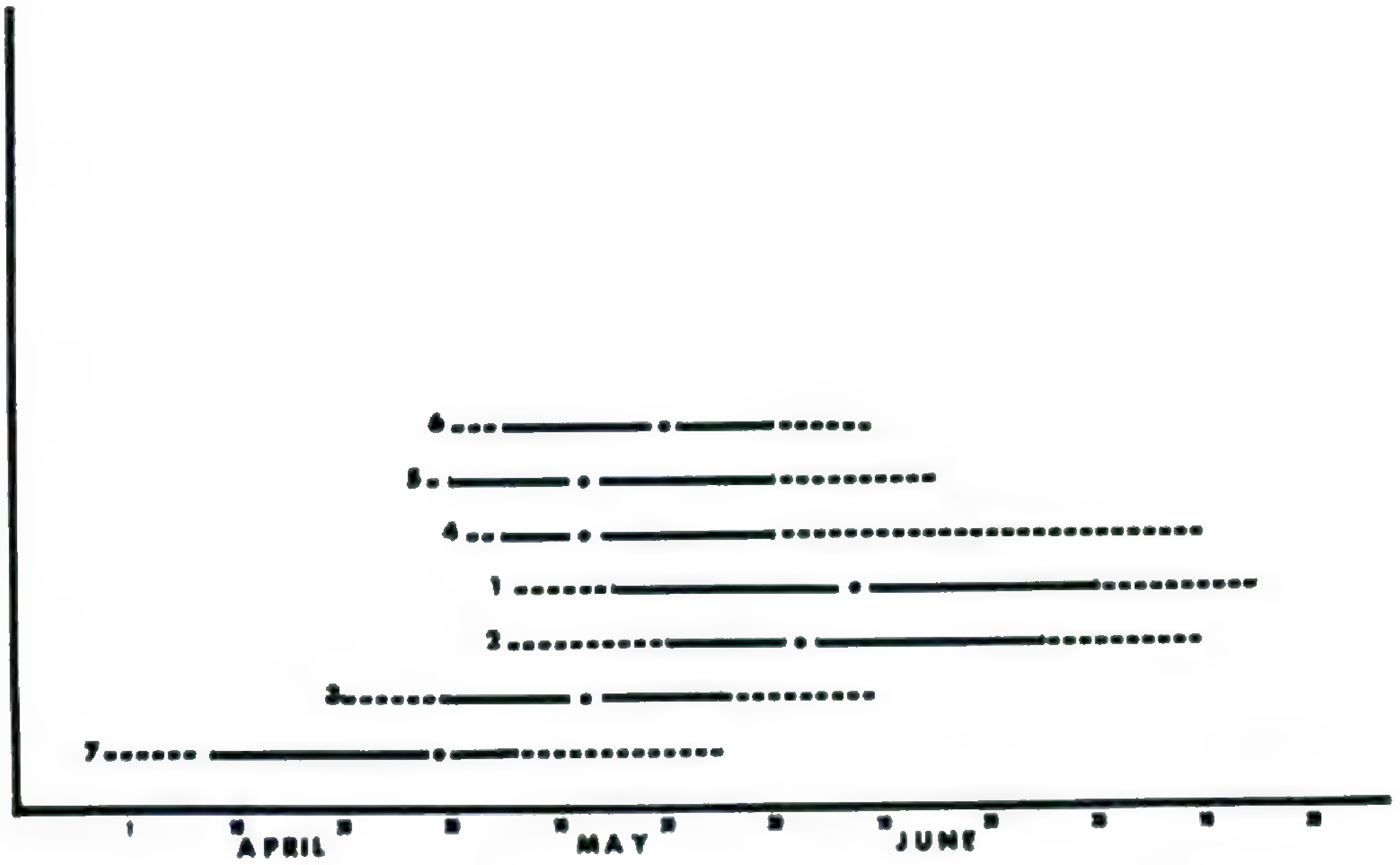


Fig. 20. Bar diagram showing the flowering interval in *Smilax* species: 1. *S. herbacea.* — 2. *S. lasioneuron* — 3. *S. pulverulenta.* — 4. *S. pseudo-china.* — 5. *S. illinoensis.* — 6. *S. ecirrhata.* — 7. *S. hugeri.* The solid black line indicates the major interval of flowering and the dark spot in the middle represents the mode The dotted lines show the interval in which flowering is irregular.

the third week of May in the Mid-central Plains to the second week of June in the northern parts. These two species have been recognised by some authors as two different varieties of *S. herbacea*. The difference in the flowering period between these two species might partly explain the rarity of intermediate forms as a result of partial or complete sexual isolation, even though both exist sympatrically in the Mid-central Plains.

Smilax herbacea reaches its peak flowering in the first week of June in the Carolinas and Virginia; it extends to the end of June in the New England States. *Smilax ecirrhata* and *S. illinoensis* reach their peak flowering in the third week of May, but *S. illinoensis* has a slightly more extended flowering period, ranging from the second week of May (Fig. 20).

POLLEN STUDIES

Pollen morphology is fairly uniform in the section. The exine is slightly spinous, 1 - 2 microns in thickness, and with no distinct furrow. Pollen size varies from 16.8 to 32.2 microns. *Smilax pseudo-china* has the smallest pollen with a mean size of 23.0 microns; the largest is that of *S. ecirrhata* with a mean value of 26.24 microns

Five plants were selected from each species and from each plant 50 pollen grains were measured at random. The mean value for each species was determined from these measurements. All together more than 2000 pollen grains from the eight species were measured.

Species		*Mean Size of Pollen*
S. herbacea	. .	24.75 microns
S. pulverulenta	. .	24.47 microns
S. lasioneuron	. .	24.48 microns
S. illinoensis	. .	25.54 microns
S. ecirrhata	. .	26.24 microns
S. hugeri	. .	24.44 microns
S. pseudo-china	. .	23.00 microns

Pollen measurements are of particular interest in three species. The mean size of pollen in *S. lasioneuron* is 24.48

microns; in *S. ecirrhata,* 26.24 microns; in *S. illinoensis,* an apparent introgressant hybrid of the preceding two, 25.54 microns.

The morphology of the tendrils in *Smilax* has long been controversial. The tendrils have been homologised with many other plant organs; modified stipules; bipartite liguils, each tendril representing a demiligule; metamorphosed trichomes or emergences. and metamorphosed leaflets of a compound leaf. After extensive anatomical and morphological studies of the tendrils in *S. herbacea,* (Agnes) Arber (1920) demonstrated conclusively that these tendrils have arisen by chorisis or dedoublement of the petiole and so are equivalent to them. Working with *S. macrophylla,* Chakravarthi and Mitra (1948) have also reached the same conclusion that the tendrils are formed by chorisis or splitting of the petiole.

MEASUREMENTS OF MORPHOLOGICAL CHARACTERS

All measurements were made from dried herbarium specimens. In all cases, the largest leaf with its axillary peduncle, if any, was selected for measurement. The leaves on the branches were not used, as they differed from those on the main stem both in shape and size.

SPECIFIC CONCEPT

The section *Coprosmanthus* stands isolated from the woody sections by the presence of the annual herbaceous unarmed shoots arising from a perennial rhizome, and biovulate carpels in contrast to the uniovulate carpels in the woody *Smilax*. Yet the differences between them are not sufficient enough to circumscribe them under two separate genera as suggested by Rafinesque (1825) and accepted by Small (1903), and so the author prefers to keep the herbaceous species under the section *Coprosmanthus* within the genus *Smilax*. The group as such has long been considered fairly distinct, the only problem being limited to the specific level. Observations of natural populations and greenhouse materials indicate that the shoots are highly sensitive to ecological variations, and show marked variation in ex-

ternal morphology, e.g., relative size of the leaves and peduncle, texure of leaves and height of the plant. In the presence of such ecological plasticity, it is likely that shoots developing from the same rhizome in different years might show morphological variation sufficient to result in the plants being considered as intraspecific categories. Therefore, prolonged observation under constant ecological conditions is necessary before attempting to designate such categories within species. No such intraspecific categories are recognised in this study.

GENERIC RELATIONSHIPS AND TAXONOMIC POSITION

The circumscription of the genus *Smilax* is generally accepted. The section *Coprosmanthus* represents a closely knit group of herbaceous species within the genus *Smilax*: smooth annual shoots from the perennial rhizomes; presence of staminodes on pistillate flowers; and the presence of biovulate carpels. The uniformity of the floral and vegetative characters is remarkable. The distinctions between the herbaceous and woody species are listed below:

	Herbaceous Smilax	*Woody Smilax*
1.	Shoots annual and herbaceous	Shoots perennial and woody
2.	Stem smooth and unarmed	Stem armed (spinous)
3.	Shoots short, erect, or up to 3 meters high and climbing	Shoots generally much taller and climbing
4.	Peduncles in general long	Peduncles mostly short
5.	Two ovules in each carpel	One ovule in each carpel

DISTRIBUTION, ECOLOGY AND EVOLUTION

The section *Coprosmanthus* has a wide distribution which extends throughout the eastern half of the North American Continent. All species prefer very moist, shady woods. *Smilax lasioneuron* thrives well even in dry soil. Most species prefer the plains. Only two species, *S. herbacea* and *S. biltmoreana,* have their distribution almost exclusively on mountains.

Smilax pseudo-china is restricted to the eastern Coastal Plain, extending from Georgia to New Jersey and southern New York. (Fig. 21). *Smilax herbacea,* like *S. biltmoreana,* prefers higher elevation and is reported as occurring

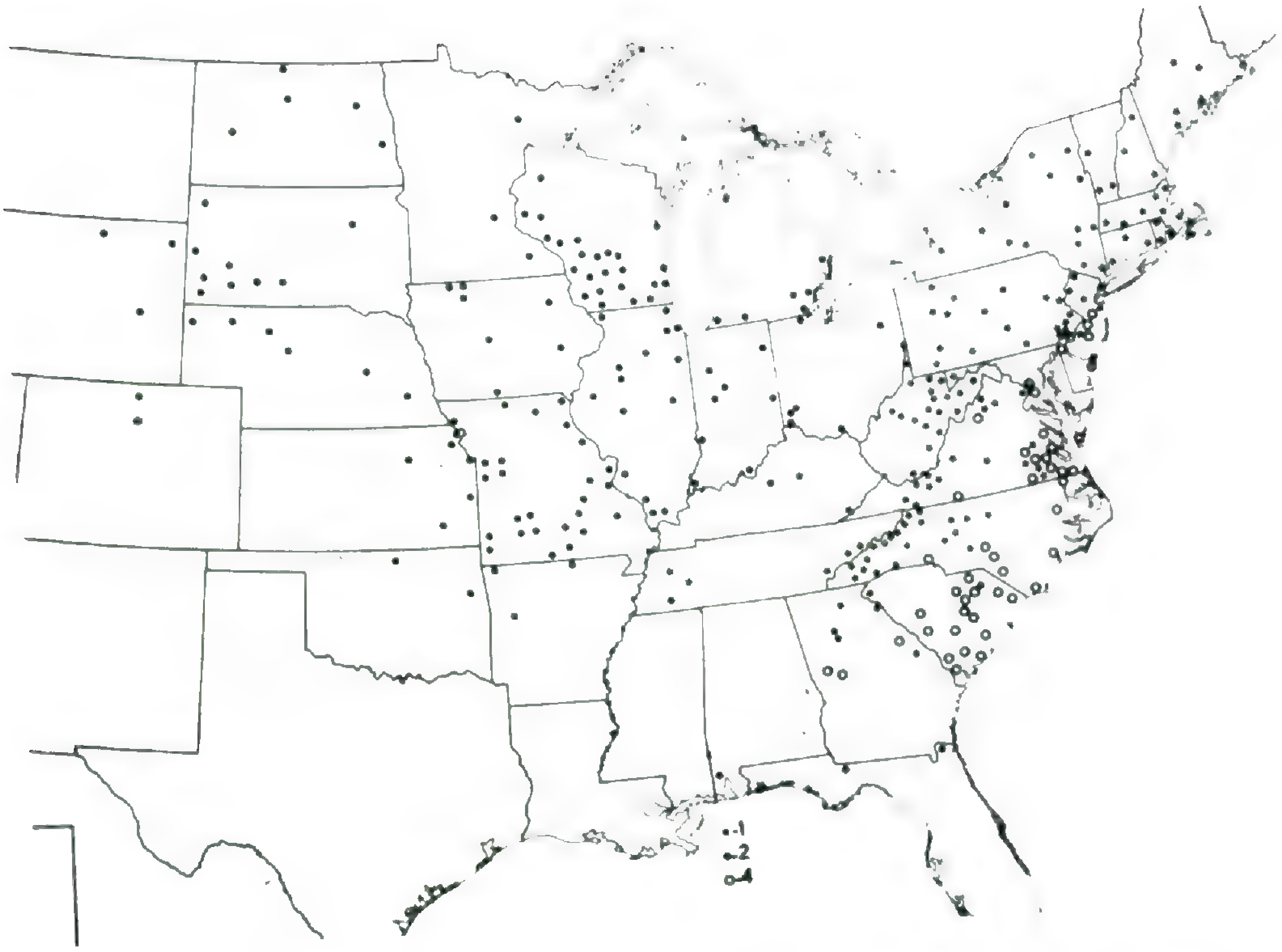


Fig. 21. Geographic distribution of *Smilax:* 1. *S. herbacea.* — 2. *S. lasioneuron.* — 4. *S. pseudo-china.*

only along the Appalachian and Blue Ridge Mountains. Thus its distribution extends from the Carolinas to the New England States and southeastern Canada (Fig. 21).

Smilax biltmoreana has a fairly restricted distribution. It is found in parts of North Carolina, South Carolina, Tennessee, Kentucky, Georgia, Alabama, and northern Florida (Fig. 23). *Smilax hugeri* has a more eastward distribution, extending to the Atlantic Coast. This species is also found in Tennessee and Kentucky (Fig. 22).

The distribution pattern of *Smilax pulverulenta* is rather unique. This species spreads across the Great Plains and reaches the Atlantic Coast through Virginia, Maryland, and New Jersey. It thus has a sympatric distribution with four other species of this section (Fig. 22).

Smilax lasioneuron is widely distributed throughout the Coastal Plains and northward into Canada (Fig. 21). The major distribution range of *S. ecirrhata* is the northern Central Plains (Fig. 23) and southern Canada.

Fig. 22. Geographic distribution of *Smilax:* 3. *S. pulverulenta.* — 5. *S. Illinoensis.* — 7. *S. hugeri.*

Smilax illinoensis is distributed mostly in the Great Lakes Region, but it also extends to northern Missouri (Fig. 22). This species, a morphological intermediate between *S. lasioneuron* and *S. ecirrhata* and identified in most

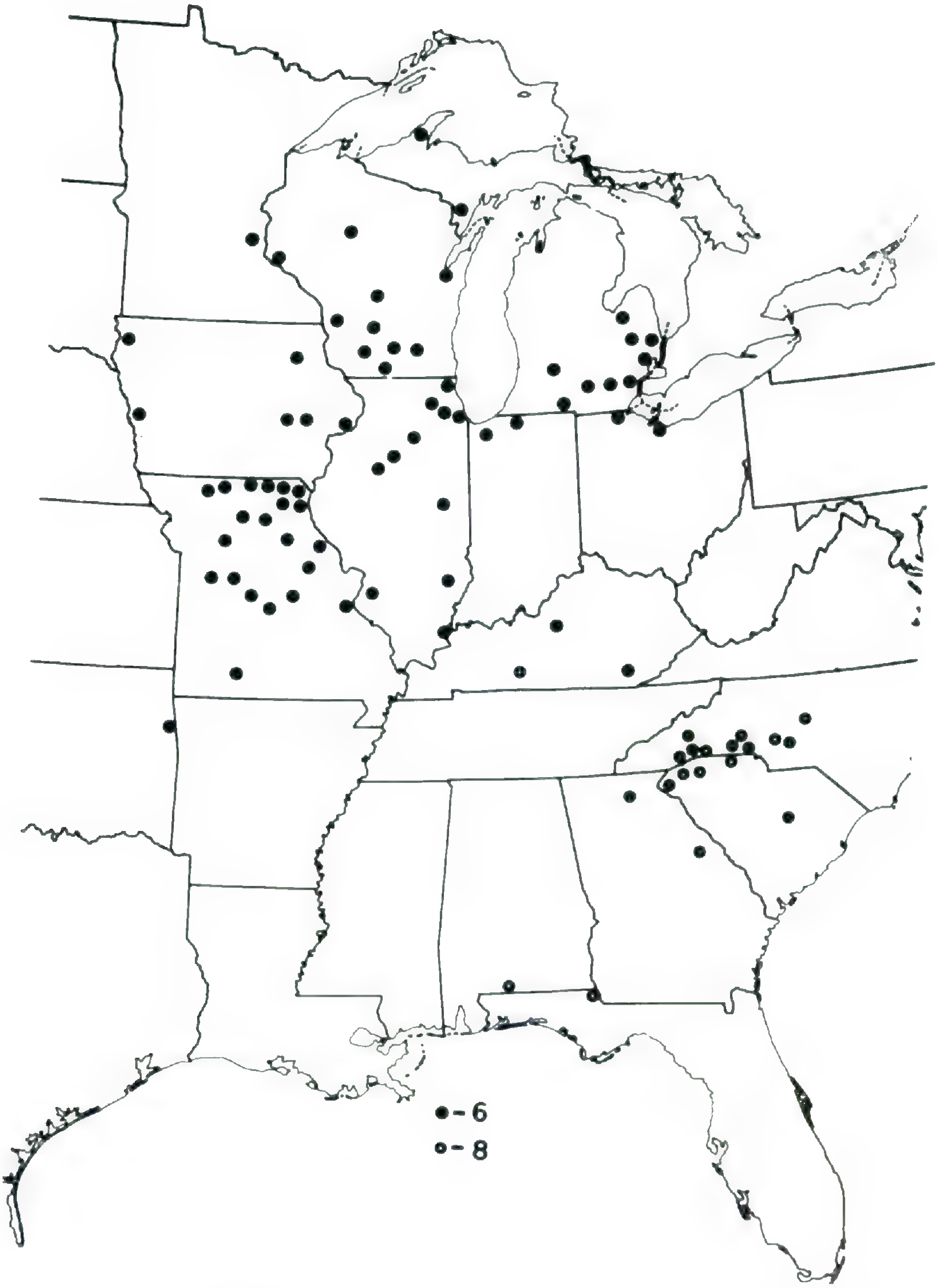
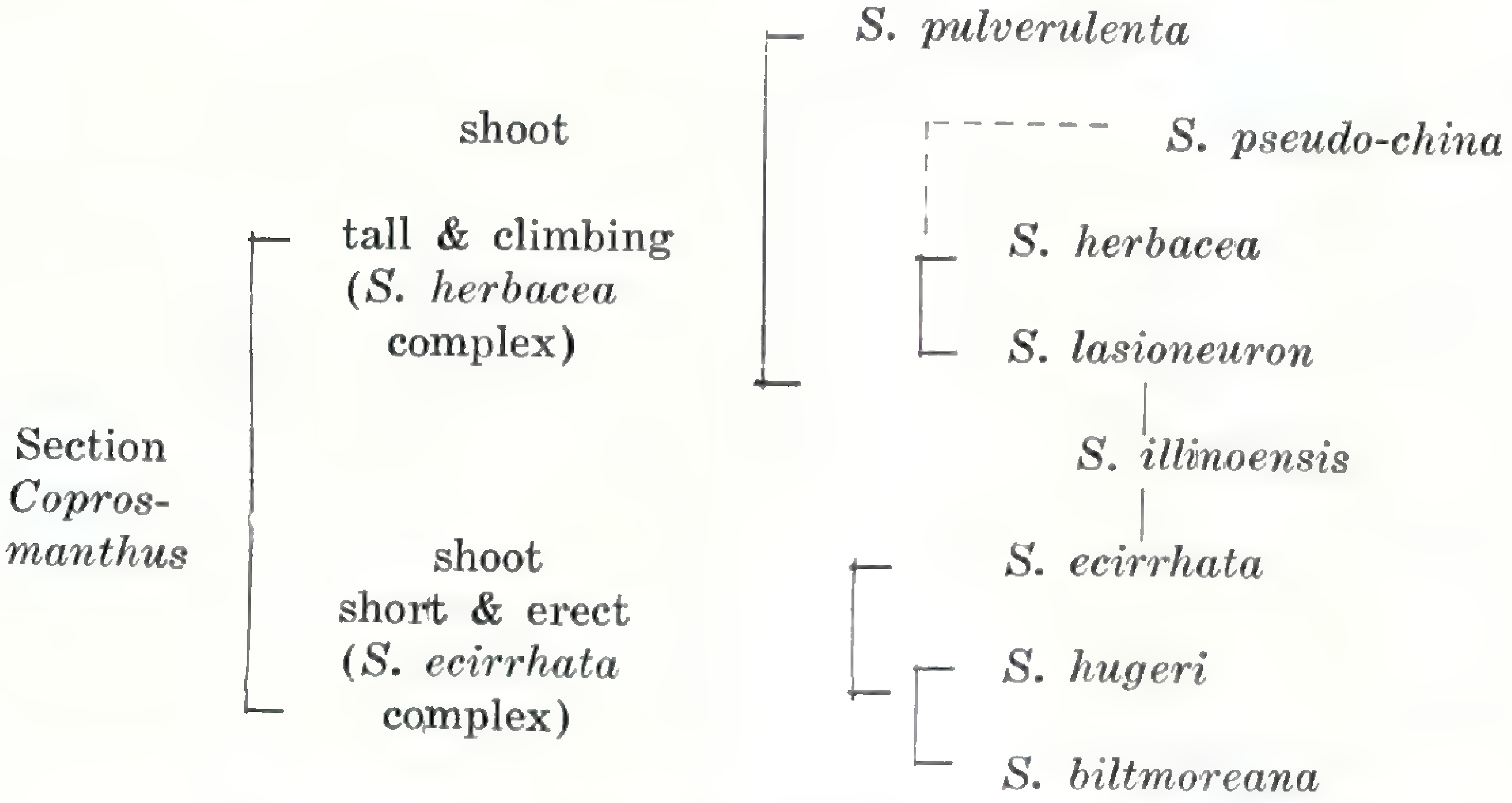


Fig. 23. Geographic distribution of *Smilax:* 6. *S. ecirrhata.* — 8. *S. biltmoreana.*

herbaria as either of these two species or both, exists sympatrically with them. The greatest concentration of *S. illinoensis* is in Wisconsin, northern Illinois and Michigan and along the northern shores of the Great Lakes.



Both paleontology and comparative morphology strongly suggest the ancestral home of *Smilax*, both herbaceous and woody, to be in southeastern Asia, east of the Himalayas. The phylogeny of the section *Coprosmanthus* is not well understood. In eastern Asia, where the genus *Smilax* might have originated, the sectional barriers generally break down. Possibly, the Asian species *S. riparia,* widespread in Japan, Korea, and China, might give some insight into the probable ancestry of the section *Coprosmanthus.* Like all other herbaceous species, *S. riparia* produces annual shoots from the rhizome throughout Japan, Korea, and northern China, but in southern China the shoots are perennial.

Basing his conclusion on fossil evidence and comparative morphology, J. B. Norton (1916) traced both the eastward and westward migration route of *Smilax* from Asia to North America. He suggested that the herbaceous species of *Smilax* reached continental North America by an eastward migration along the path of *S. hispida,* by island hopping across the Pacific. These migrant ancestral forms might have been fairly well established in the central California region in Late Miocene or in Early Pliocene (Fig.

24). Any suggestion as to the establishment, further migration, and diversification of the group, in the absence of conclusive fossil evidence, remains purely hypothetical.

Fossil evidence of the vegetation both in Miocene and Mid-Pliocene indicate that in California both these epochs were comparatively dry and warm with a summer rainfall of 15 - 17 inches and the vegetation appears to have been similar to that of the present vegetation in this region. However, in the early Pliocene the climate was more or less equivalent to the present climate of eastern North America, and eastern Asia, with a minimum summer rainfall estimated to have been 25 - 30 inches (Axelrod, 1948). Such a moderate humid climate is ideal for *Smilax* and its presence in the California region during the Early Pliocene has been established by fossil evidence.

During the Middle Pliocene, when the climate became progressively warmer and drier, a general eastward migration might have occurred. Fossil evidence in western Kansas and Nebraska indicates clearly that the Middle Pliocene was the stage of greatest diversification of fossil types in contrast to the gradual changes in Miocene and Early Pliocene floras. Post Middle Pliocene was a time of large-scale mountain building, and as a result, a great diversification of the topography and habitat occurred. Added to that, the fluctuating Pleistocene climate kept the entire area in a continuous flux for a long time (Axelrod, 1948). This might have resulted in further diversification of the group that continues to the present time.

Whether the divergence of the section *Coprosmanthus* into the tall *Smilax herbacea* complex and the short *S. ecirrhata* complex was completed in Asia itself or the divergence occurred in continental North America is uncertain. This differentiation was probably distinct by the time the herbaceous species became established in Kansas and Nebraska during Late Pliocene. Probably at this time or even earlier, further diversification had already begun in the *S. herbacea* complex, with one branch providing the precursors of *S. pulverulenta* (Fig. 24). This new species

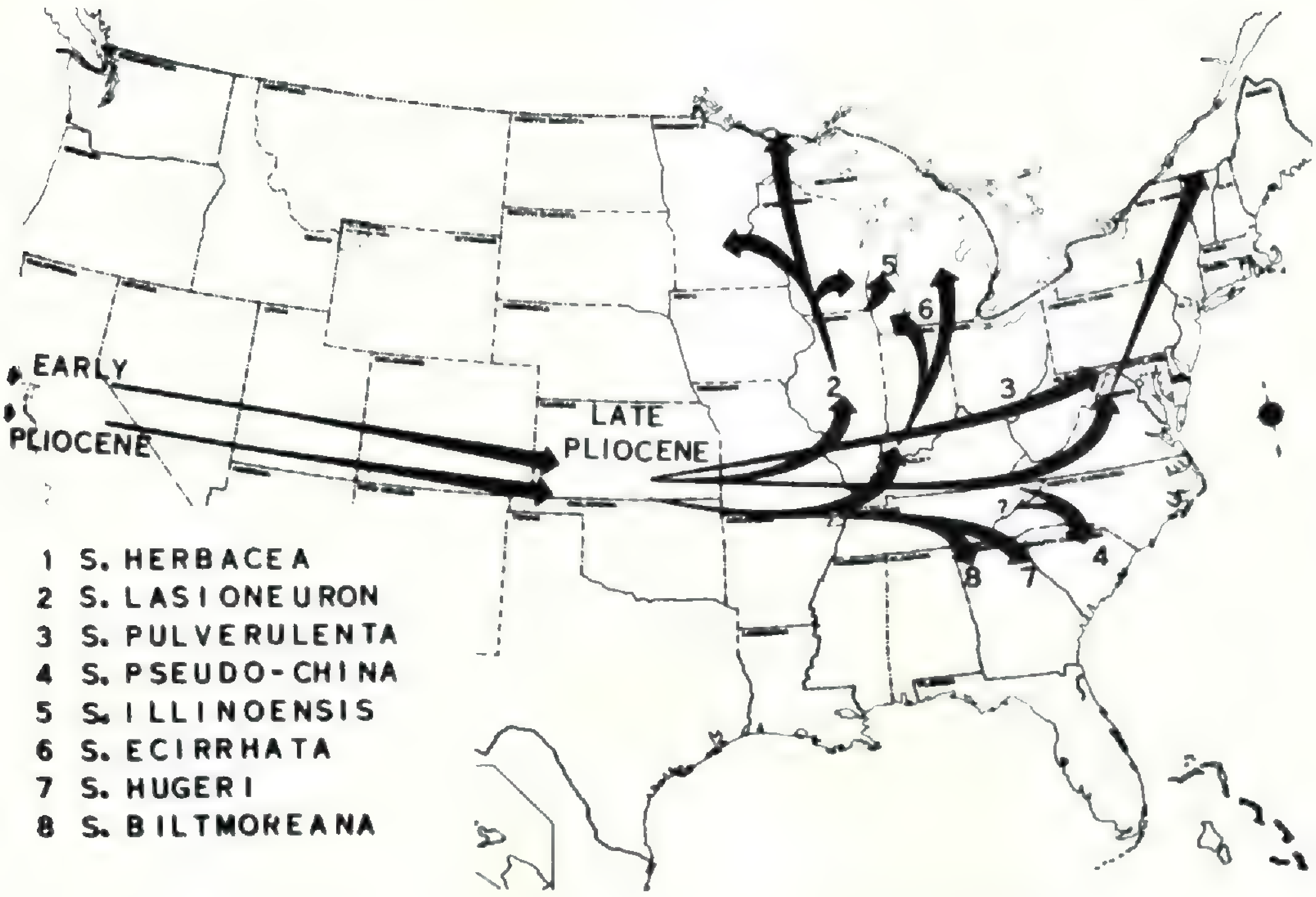


Fig. 24. Possible migration routes and diversification of herbaceous *Smilax* on Continental North America.

gradually spread further eastward and northward, eventually reaching the Atlantic Coast.

The other branch of *S. herbacea* complex also continued the general eastward migration and soon bifurcated. One branch, the ancestral forms of *S. lasioneuron,* spread mostly northward into Canada as the Pleistocene glaciers receded. The other branch, progenitor of *S. herbacea,* reached the Blue Ridge Mountains and spread northward all the way to eastern Canada along the Appalachian Mountains.

The phylogeny of *Smilax pseudo-china* is not clear. However, the morphological resemblance of this species to *S. herbacea* and the presence of higher chromosome numbers provide a working hypothesis that *S. pseudo-china* originated by interspecific hybridization of *S. herbacea* with some other *Smilax* species.

The other major group, the ancestral forms of *Smilax ecirrhata* complex, also first diverged into two groups. One branch, the fore-runners of *S. ecirrhata,* slowly spread northward in the same direction of *S. lasioneuron* and be-

Fig. 25. A. *Smilax illinoensis* and B. *Smilax ecirrhata.*

came established in the northern central plains towards the end of Pleistocene. Hybridization might have been fairly common between these two sympatric species. In suitable habitats around the Great Lakes, these hybrids, by further introgression, formed *S. illinoensis.*

The other branch of the *Smilax ecirrhata* complex continued to migrate eastwards into Tennessee and Kentucky and slowly diverged into two groups. One group, the progenitors of *S. biltmoreana,* spread along the mountains in Tennessee, Kentucky, the Carolinas, and Georgia. The other group migrated further eastward into the Carolinas and evolved into *S. hugeri.* In western Tennessee and Kentucky, the species differences of the *S. ecirrhata* complex are not as sharp as elsewhere, suggesting that the divergence of this complex probably occurred in this region.

Following is the list of herbaria from which specimens were borrowed during this study. The abbreviations used in citation of specimens are those recommended by Lanjouw and Stafleu (1963).

Ann Arbor, Michigan; University Herbarium, University of Michigan (MICH)

Athens, Georgia; Herbarium of the University of Georgia (GA)

Austin, Texas; Herbarium of the University of Texas (TEX)

Cambridge, Massachusetts; Arnold Arboretum of Harvard University (A)

Cambridge, Massachusetts; Gray Herbarium of Harvard University (GH)

Chapel Hill, North Carolina; Herbarium of University of North Carolina (NCU)

Chicago, Illinois; Field Museum of Natural History (F)

Gainesville, Florida; Herbarium, Agricultural Experiment Station (FLAS)

Knoxville, Tennessee; Herbarium of the University of Tennessee (TENN)

Laramie, Wyoming; Rocky Mountain Herbarium, University of Wyoming (RM)

Madison, Wisconsin; Herbarium of the University of Wisconsin (WIS)

Morgantown, West Virginia; Herbarium of West Virginia University (WVA)

New York, New York; New York Botanical Garden (NY)
Philadelphia, Pennsylvania; University of Pennsylvania Herbarium (PENN)
Philadelphia, Pennsylvania; Academy of Natural Sciences (PH)
St. Louis, Missouri; Missouri Botanical Garden (MO)
Tallahassee, Florida; Herbarium, Florida State University (FSU)
Washington, D.C.; Herbarium, Catholic University of America (LCU)
Washington, D.C.; National Museum, Smithsonian Institute (US)

TO BE CONTINUED

VARIATION IN CONE MORPHOLOGY OF BALSAM FIR, ABIES BALSAMEA[1]

DONALD T. LESTER

Balsam fir, *Abies balsamea* (L.) Miller, is a widely distributed forest tree species in North America. The extent of its distribution is problematical in that Boivin (1959) has proposed the reclassification of the alpine fir of western United States and Canada, *A. lasiocarpa*, as a subspecies of balsam fir. Such reclassification would markedly extend the natural range and the amount of variation in taxonomic characteristics currently recognized within *A. balsamea.*

Considering only the more eastern taxon (Figure 1) as *A. balsamea* (L.) Miller, recognition of variation in the species has been largely restricted to observations on the relationship between the length of cone scales and the length of the bract that subtends each cone scale. Taxonomic identification of variation in balsam fir was proposed by Fernald (1909) with assignment of the varietal name *phanerolepis* to variants in which bracts were sufficiently long to be exposed in the mature cone (exserted). The variety *phanerolepis* has been shown to be most common in the Maritime Provinces of Canada, the St. Lawrence Valley, and at higher altitudes on mountains of the northeastern United States (Fernald, 1950; Myers and Bormann, 1963). The scale-bract relationship has been the chief characteristic used in maintaining Fernald's varietal distinction. Boivin (1959) noted the absence of discontinuities in the bract-length/cone scale length ratio in a sample of cones from Quebec but maintained the variety *phanerolepis* in his classification. Myers and Bormann (1963) reported altitudinal and longitudinal gradients in the scale/bract ratio and questioned the taxonomic validity of variety *phanerolepis.*

[1]Work supported in part by the North Central Regional Project, NC-51, and the Wisconsin Conservation Department. Approved for publication by the Director, Wisconsin Agricultural Experiment Station.

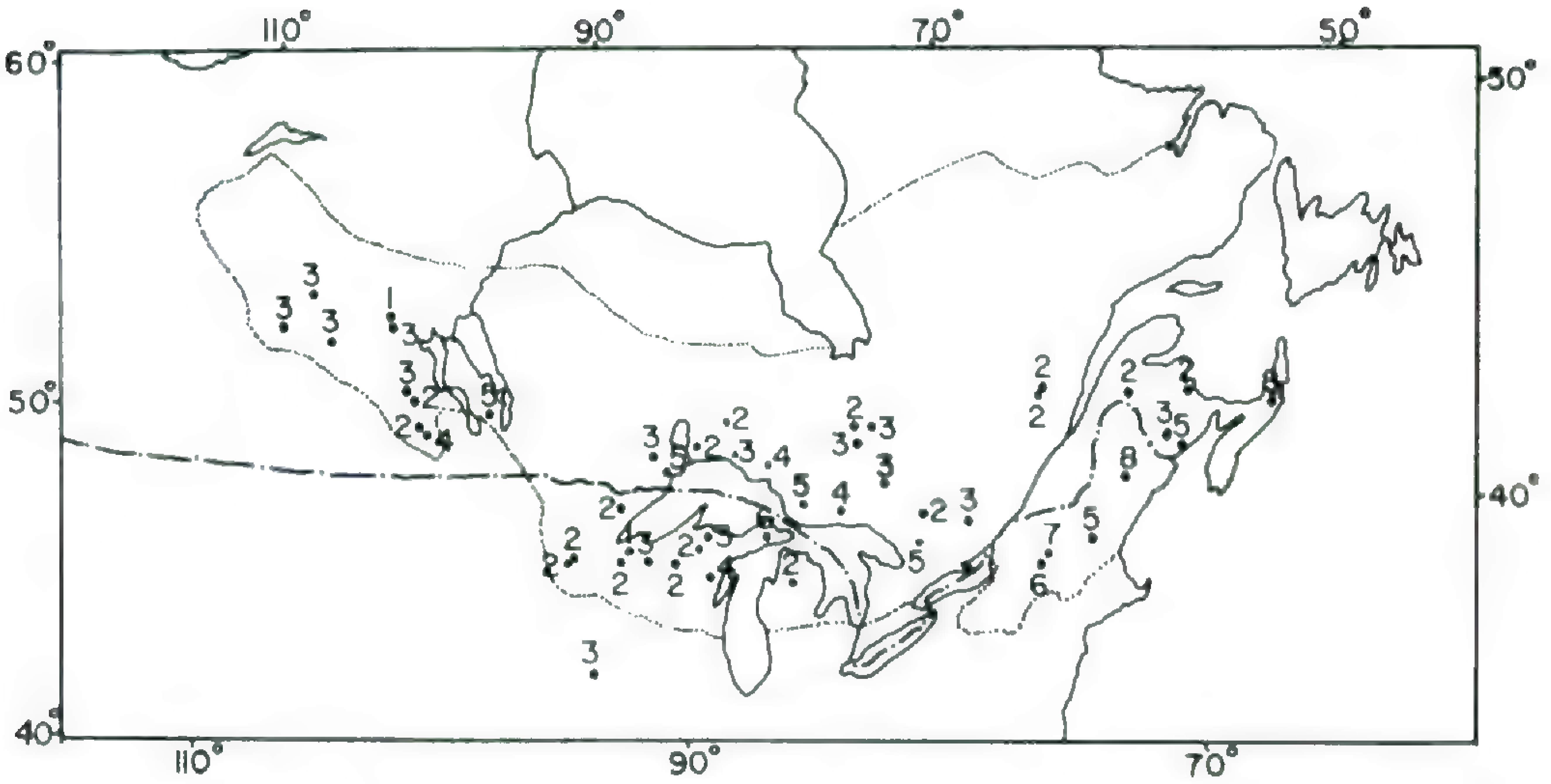


Figure 1. Natural range of balsam fir (. . . .), location of collections (.), and score of bract length/scale length ratios. Scores represent eight equal subdivisions of the array of ratios ranging from .44 to .80.

The study reported here represents a westward extension of the area sampled in earlier studies, a more intensive study of variation in cone morphology of balsam fir, and analyses of possible associations between variation in cone morphology and climatic variables. This study is a part of investigations of variation in balsam fir which include seed source or provenance tests currently in progress.

METHODS

In the period 1960 to 1966, seed collections of balsam fir were made by personnel of the University of Wisconsin and by cooperators in the United States and Canada. One hundred populations representing much of the readily accessible natural range were sampled. As an adjunct to the collection of cones for seed, intact cones from 49 populations (Figure 1) were preserved in formalin-acetic acid-alcohol solution. Ten of the cone collections were made in 1960 (northern Wisconsin and Michigan), 41 in 1962, one (Iowa) in 1964, and 5 in 1966. Elevations of the collections were generally within the range of 500 to 2000 feet although one New York collection came from an elevation of 3600 feet. Two cones, randomly chosen from each tree, were preserved and

from two to ten trees were sampled at each location. Sample trees generally were scattered over an area of a few acres although some sample trees were separated by distances of up to three or four miles.

On each cone, cone width at the widest point and cone length were measured. Three cone scales were then removed from the middle of each cone for the measurements illustrated in Figure 2. These measurements were made using an ocular micrometer in a dissecting microscope.

Ten variables were studied. Measurements of length of cone, ovuliferous scale, seed wing, and bract were analysed

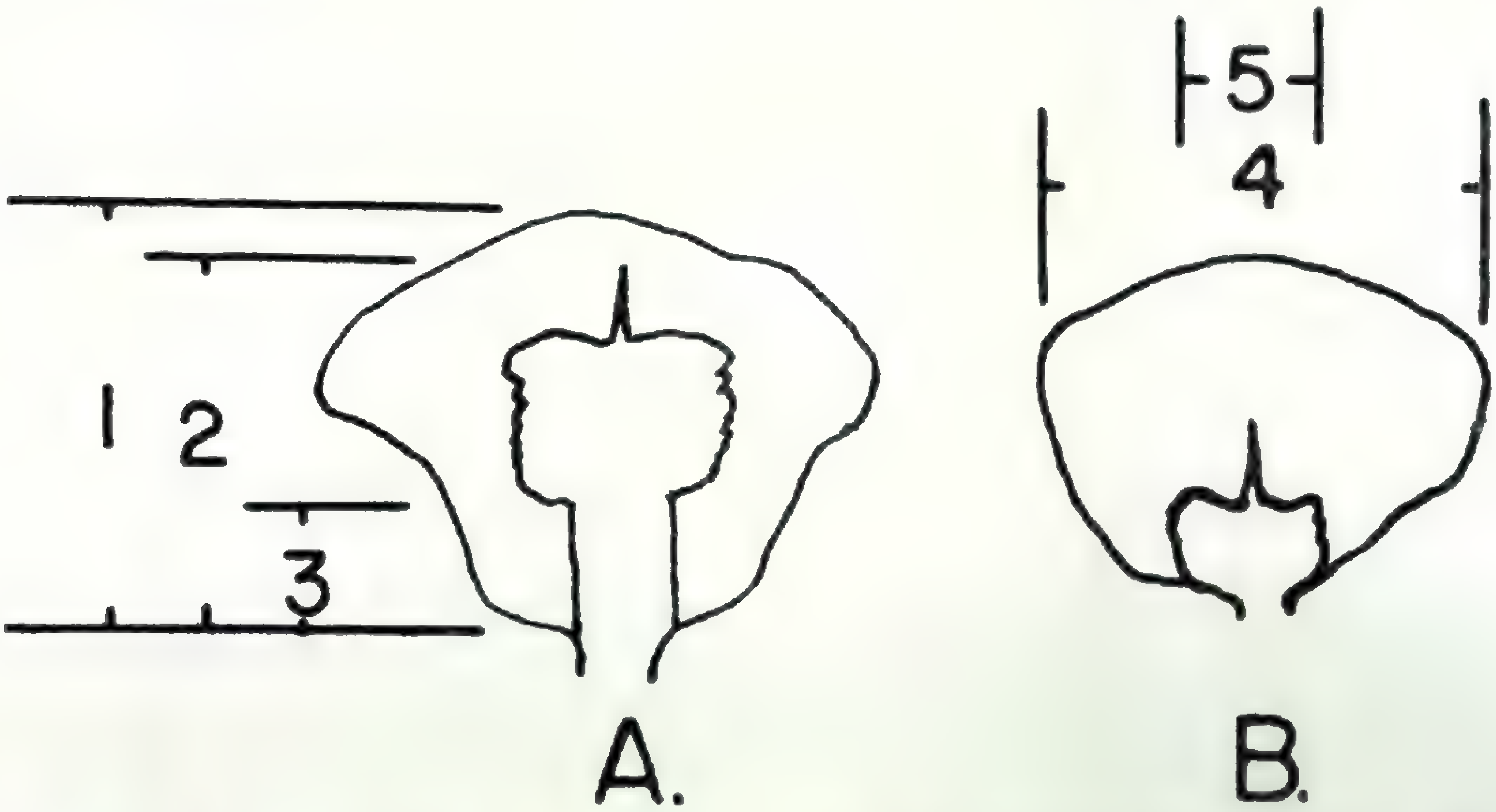


Figure 2. Sketches of abaxial view of ovuliferous scales and bracts. A. Maine collection, bract-scale ratio is .85. B. Western Ontario collection, bract-scale ratio is .50. Indicated measurements are 1. scale length, 2. bract length, 3. stalk length, 4. scale width, and 5. bract width.

directly. Due to the high frequency of zero, values for stalk length were transformed to $\sqrt{x + 0.5}$ before analysis. Ratios of length/width were calculated and analysed for cones, scales, wings, and bracts, along with the ratio bract length/scale length as a measure of bract exsertion.

Four sources of variation were hypothesized; variation associated with geographic location, with differences between trees in locations, with differences between cones within trees, and with differences among measurements

within cones. Analyses of variance (Table II) were used to estimate whether each of the proposed sources of variation contributed significantly to the total variation. The relative contribution of each source was estimated by extension of the analysis of variance to computation of variance components.

Speculative associations between cone morphology and climatic variables were tested by linear correlation using mean values for each geographic location and for weather data from the station nearest to the collection location. Long-term averages were used; the period of recorded observations being 30 years for temperature and precipitation, and generally 10 years or more for frost-free period. Proximity of weather stations to cone collections was sometimes poor with distances being up to 50 miles in northern and western regions.

RESULTS

VARIATION IN CONE MORPHOLOGY

A sample of the arrays of average measurements for each location illustrate several points about variation in cone morphology in balsam fir (Table I). The arrays show a generally continuous pattern of variation with the exception of one New Brunswick collection in which length of the ovuliferous scale was significantly greater (99% probability) than in any other location. Although collections from the eastern portion of the sampled range were mostly among those with the longest cones, no clear geographic grouping was apparent for most of the characteristics measured.

Cone length was chosen as the variable with which to organize the sample of arrays in Table I. It was expected that development of cone parts, with the possible exception of bracts, would be strongly correlated with cone length so that the arrays for all characteristics might be similar. From Table I it is apparent that although longer cones generally had longer scales, seed wings, and bracts, substantial variation independent of cone length was present. For example, average cone length for the Maine collection was significantly longer than for either Wisconsin collec-

tion and yet no significant differences were apparent in scale or seed wing length for the three locations. Ratios of length/width showed less relation to cone size than length measurements, suggesting that differences in the shape of cone parts were not primarily functions of cone length.

The ratio of particular interest was bract length/scale length. For this ratio a geographic grouping of high values in the eastern portion of the range is apparent (Figure 1). The arrangement of scales in the fir cone is such that portions of the bract are generally visible when the bract length/scale length ratio exceeds 0.8 to 0.9. The highest average ratio for a location was 0.8 for the Nova Scotia collection. This value is appreciably less than the ratio of 0.9 suggested by Boivin (1959) or 1.0 suggested by Fernald (1909) for identifying the variety *phanerolepis*. However, the average ratio of measurements for one tree in the Nova Scotia collection exceeded 0.9 and the maximum value for a single measurement was 1.0. These observations emphasize the tree-to-tree variation as well as within cone variation for some cone characteristics.

COMPONENTS OF VARIATION

The analyses of variance indicated that locations, trees within locations, and cones within trees all contributed significantly (at 99% probability) to the observed variation in all measurements and ratios. The relative contributions of each source of variation are summarized in Table II.

Variation in cone length was associated approximately equally with differences between locations, between trees within locations and between cones within trees. For the other measurements, the predominant sources of variation were differences between geographic locations and between trees within locations. Variation associated with location was pronounced for bract and stalk length while tree-to-tree variation was predominant in length/width ratios with the exception of the ratio for bracts.

Variation associated with differences between cones from the same tree was relatively small in measurements of cone parts and in ratios. This suggests that except for measures

of cone size, a small sample of cones from a given tree will accurately reflect the floral morphology of that tree.

Variation associated with samples from the same cone was either small or large depending on the variable considered. Restricting the sampling to the mid-portion of each cone unquestionably reduced sampling variation because ovuliferous scales at either end of the cone are smaller than in the middle. Bract length/scale length ratios also vary somewhat from base to tip of the cone. Variation within cones is thus probably greater for all characteristics measured than variation between cones from the same tree.

The predominance of geographic effects on variation in bract and stalk length suggests that bract development is of primary importance in relation to geographic distribution of balsam firs with different bract/scale ratios. During measurement of cone parts, it seemed that variation in stalk length might be contributing in a major way to variation in bract length. To test this speculation, the contributions of variation in stalk length and in blade length to variation in total bract length were estimated. Average values for geographic locations were used in multiple regression analysis. Contrary to impressions during measurement, the analysis revealed that variation in stalk length contributed only about 17% more than variation in blade length.

CORRELATION WITH CLIMATIC VARIABLES

The possible association of variation in cone morphology with certain climatic variables was tested by simple correlation. Frost-free period, mean annual temperature and precipitation, and mean monthly temperatures for May, June, and July were the climatic variables used. Table IV summarizes the statistically significant correlations and illustrates the association of bract development with climate. In view of the impossibility of obtaining weather data known to be representative of the collection location, the correlations must be interpreted with particular caution. Yet, the moderate correlation between bract characteristics and mean annual temperature and precipitation fits well with other analyses in which geographic location of the cone collection

was shown to be the predominant source of variation in bract length.

DISCUSSION

Studies of variation in samples from native populations represent one type of approach to describing variation within species. These studies can complement experiments on comparative genetics and physiology conducted through the common-environment approach. Sampling in native populations commonly emphasizes structures which are less easily modified by environment so that the observed pattern of variation may more closely resemble patterns of genetic variation. Floral characters are generally less subject to environmental modification, perhaps as a result of differentiation and development of primordia over relatively short periods of time (Stebbins, 1950). Cones have been the structures of chief interest in studies of variation in balsam fir.

In the present study, samples from much of the readily accessible range of the species have shown generally continuous variation in measurements on cones and cone parts, as well as in measures of shape by length/width ratios. The continuity of variation, however, did not reflect a completely random pattern of geographic distribution. The more eastern collections were generally grouped near the top of some arrays, particularly those involving characteristics of the bract. The apparent association of variation in some cone characters with precipitation and temperature suggests that the grouping of eastern collections may be a reflection of climatic characteristics in the eastern portion of the range. It might be expected, therefore, that in other portions of the range, variation in local climates or years of unusually heavy rainfall at critical stages in cone initiation or development could produce similar variation.

On the other hand, the major contribution of trees within locations to total variation suggests that genetic differences or local environment associated with soil differences, crown position, or stand density could cause much of the observed variation. Fernald (1909), in proposing the variety *phan-*

erolepis, noted that trees bearing cones with exserted bracts were growing intermingled among trees of the species type at Percé Mountain on the Gaspé Peninsula. Myers and Bormann (1963) similarly found trees characterized by cone scale/bract ratios ranging from variety *phanerolepis* to variety *balsamea* within the St. Lawrence Valley, Gaspé Peninsula, and Maine, although from their data it is not clear whether the whole range of variation was present in any one small group of trees.

Possible genetic control of variation in the bract/scale ratio is suggested by comparison of the cones of variety *phanerolepis* with *A. fraseri*, a species currently restricted to high elevations in the Southern Appalachian Mountains. Cones of *A. fraseri* are characterised by exserted and strongly reflexed bracts wherever the species is grown. In *A. balsamea*, altitudinal clines for the cone scale/bract ratio have been demonstrated, with exserted bracts being predominant at the highest elevations (Myers and Bormann, 1963). In *A. fraseri*, gene fixation for bract development may have resulted from restriction of the species to high elevations following a xerothermic or hypsithermal period (Mark, 1958). In *A. balsamea* the high elevation gene pool remains connected to lowland populations. The relative contributions of environment and genetic differentiation to variation in cone morphology of *A. balsamea* eventually should be estimable in the common-environment experiments now in progress.

The influence of geographical location of cone collection was most evident in the variation in bract length. Although the correlations in Table IV must be viewed with particular caution, the apparent moderate association of bract length with mean annual temperature and mean annual precipitation coincide with the indicated influence of geographic location. Variation in the developmental pattern of bracts may thus be the basis for the variety *phanerolepis*.

Fernald (1950) defined a variety as "a strongly fixed variation of a species with the essential reproductive parts unchanged but showing somewhat constant departures in

size of parts, shape of leaves, or modification of the less fundamental parts of the flower, etc. and occupying a somewhat segregated geographic area". If distinct discontinuity in the pattern of variation is not a prerequisite for varietal classification, Fernald's definition seems most questionable on the point of "a strongly fixed variation . . . showing somewhat constant departures . . .". The separation of genetic and environmental influences on bract development will be necessary to establish how strongly fixed and how constant is variation in bract development. Assignment of a bract length/cone scale length ratio of about 0.9, or, more simply, assigning trees bearing cones with exserted bracts to variety *phanerolepis,* will result in a geographic subdivision of the species range. Within that subdivision the frequency of trees classified as the variety *phanerolepis* will vary continuously along altitudinal and geographic gradients and perhaps from year to year. Varietal classification here serves merely to recognize an arbitrary, though visually prominent, point on a scale of continuous variation.

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DEPARTMENT OF FORESTRY
UNIVERSITY OF WISCONSIN
MADISON, WISCONSIN 53706

Table I. Sample of arrays of mean value for geographic locations.

Geographic Location		Lengths (mm) Cone	Scale	Seed Wing	Bract	Stalk	Ratios Length/Width Cone	Scale	Seed Wing	Bract	Bract Length/ Scale Length
New Brunswick	45°58′N, 66°22′W	68.1	16.4	15.9	8.5	2.1	3.0	.87	2.3	1.4	.57
Maine	44°45′ , 68°37′	63.2	11.6	13.8	9.1	2.5	3.1	.71	2.3	1.7	.79
New Brunswick	45°35′ , 66°19′	62.4	13.2	15.2	8.5	2.1	2.7	.73	2.2	1.5	.65
New York	44°19′ , 73°55′	59.0	11.6	14.0	9.0	3.6	2.6	.69	2.2	1.5	.78
Ontario	46°25′ , 79°10′	57.2	11.7	13.9	5.9	0.8	3.2	.76	2.2	1.2	.51
New York	43°45′ , 74°07′	56.6	11.8	14.2	8.2	2.3	2.8	.71	2.1	1.5	.70
Overall Mean		51.9	11.1	13.0	6.3	0.8	2.8	.75	2.2	1.3	.57
Ontario	49°10′ , 80°15′	45.7	9.4	11.5	5.0	0.7	2.9	.68	2.1	1.2	.54
Nova Scotia	46°23′ , 60°40′	44.8	8.1	9.9	6.6	1.8	2.4	.56	2.0	1.0	.80
Wisconsin	45°58′ , 90°07′	44.7	9.5	11.8	5.2	0.7	2.6	.73	2.2	1.2	.56
Wisconsin	46°02′ , 89°32′	42.0	10.3	12.1	5.4	0.8	2.6	.76	2.2	1.2	.52
Saskatchewan	53°55′ ,101°15′	41.6	9.8	11.6	5.3	0.7	2.4	.75	2.1	1.2	.55
New Brunswick	47°05′ , 65°28′	35.0	9.6	11.2	4.8	0.7	2.0	.67	2.1	1.0	.51
Approximate significant difference with 99% probability (from Duncan, 1955 with p = 25)		11.0	2.6	2.3	1.2	0.2	0.5	0.14	0.3	0.2	0.14

Table II. Summary of analyses of variance.

A. General form of analysis

Source of Variation	Degrees of Freedom	Expected Mean Squares
Geographic Location	48	$\sigma_m^2 + C_1\sigma_c^2 + C_2\sigma_t^2 + C_3\sigma_l^2$
Trees in Location	256	$\sigma_m^2 + C_1\sigma_c^2 + C_2\sigma_t^2$
Cones in Trees	299	$\sigma_m^2 + C_1\sigma_c^2$
Measurements in Cones	1206	σ_m^2

$\sigma_m^2, \sigma_c^2, \sigma_t^2, \sigma_l^2$ = components of variance associated with measurements, cones, trees, and locations respectively.

C_1 = Mean number of measurements per cone = 3.0
C_2 = Mean number of measurements per tree = 5.9
C_3 = Mean number of measurements per location = 36.8

B. Components of variance expressed as a percentage of total variance.

Source of Variation	Length					Length/Width Ratio				
	Cone	Scale	Seed Wing	Bract	Stalk	Cone	Scale	Wing	Bract	Bract L/ Stalk L
Geographic Location	31	36	35	58	47	21	14	14	39	38
Trees in Location	39	49	42	26	28	49	40	44	36	36
Cones in Trees	30	11	17	8	9	30	5	13	8	10
Measurement in Cones	—	4	6	7	15	—	40	28	16	16

Table III. Correlation of cone measurements with measures of climate.

Cone Measurement	Annual Precipitation	Annual Temperature
Scale Length (L)	—.01	—.01
Length/Width (L/W)	.38**	—.20
Bract L	.35**	.29*
L/W	.12	.42**
Stalk L	.61**	.46**
Bract L/Scale L	.43**	.35**

* correlation coefficient differs significantly from 0 with 95% probability

** correlation coefficient differs significantly from 0 with 99% probability

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A CYTOTAXONOMIC STUDY IN VERBESINA (COMPOSITAE)[1]

JAMES R. COLEMAN[2]

In their comprehensive revision of *Verbesina* Robinson and Greenman (1899) recognized 109 species in 12 sections, 4 of which they considered as provisional, unnatural units. During this century Blake (1925) revised section *Lipactinia* and Coleman (1964, 1966a, 1966b) has recently treated 3 others. However since Robinson and Greenman's revision the number of species assigned to *Verbesina* has more than doubled because of descriptions of new species and transfers made into the genus. As a result, the relationships of many species are uncertain and sectional limits have become increasingly obscured. In an attempt to better determine specific relationships and sectional limits, a study of chromosome numbers and crossing relationships is being conducted. This paper represents the initial report on this study.

MATERIALS AND METHODS

The material utilized in this study is listed in Table 1. Voucher specimens are deposited in the herbarium of Indiana University. Crosses were made by rubbing together heads of the individuals being crossed for 2-4 consecutive days to insure that all florets had opened and were pollinated. The crosses were made in insect-free greenhouses at Indiana University with 2-5 plants generally being involved in each series of crosses. Immature heads were fixed in a solution of 95% ethyl alcohol, chloroform and propionic acid (6:2:2) (Jackson 1962). Entire florets were smeared and stained with acetocarmine. Many slides were made permanent with venetian turpentine; selected cells were

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drawn with the aid of a camera lucida. Pollen stainability, taken as a measure of viability, is based on counts of not less than 200 randomly selected grains after having been stained in cotton blue for at least 24 hours. Grains which stained deeply were considered viable; those which stained lightly or not at all were considered inviable.

CHROMOSOME COUNTS

With the addition of the counts presented in this paper, the number of species of *Verbesina* counted is increased to 29, representing about 15% of the genus. Of the 11 species counts here presented, 4 are for previously unreported species. The counts determined for the material included in this study are given in Table 1.

The count of $n = 34$ for *V. alternifolia* and $n = 17$ for *V. occidentalis* are in agreement with previous reports for these species (Heiser & Smith 1955) as are the counts of $n = 17$ for *V. lindenii* and *V. serrata* (Turner, Ellison & King 1961; Turner, Beaman & Rock 1961). Turner and Flyr (1966) report *V. warei* as $n =$ ca 17. A definite report of $n = 17$ is here reported for *V. warei*. The previously unreported species *V. aristata*, *V. longifolia*, *V. rothrockii* and *V. virginica* were determined as having $n = 17$.

Of the species of *Verbesina* thus far reported, 1 has $n = 16$ (Turner, Beaman & Rock 1961), 2 have $n = 18$ (Turner, Ellison & King 1961; DeJong & Longpre 1963) and 3 are tetraploid with $n = 34$ (Heiser & Smith 1955; Coleman 1966b; Turner & Flyr 1966). All other reported species have $n = 17$. A single species, *V. oligocephala*, is reported to have B chromosomes (Coleman 1966a). It would appear very probable that $n = 17$ is in the primitive condition in *Verbesina* and that both aneuploidy and polyploidy have played a role in the evolution of the genus.

CROSSING PROGRAM

The source of the material utilized in the crossing program is listed in Table 1. The crosses made and the results obtained are listed in Table 2. Table 3 presents the pollen stainability and meiotic behavior observed in the hybrids.

Intrasectional crosses: Only 2 sections, *Pterophyton* and

Verbesinaria, are represented by more than a single species in the crossing program. The 3 species of sect. *Pterophyton*, *V. aristata*, *V. rothrockii* and *V. warei*, were crossed in every possible combination. The cross *V. warei* × *V. aristata* and its reciprocal both resulted in high seed set; however those of the reciprocal were not grown to maturity. The hybrids displayed intermediacy for several characters. *Verbesina aristata* has an erect habit, rayed heads and numerous disk florets (ca 40-45) whereas *V. warei* is lax-stemmed, rayless and has much fewer disk florets (ca 13-25). The hybrids were intermediate for erectness of stems and possessed rayed heads with numerous disk florets similar to the male parent.

The high pollen stainability of the hybrids as well as the occurrence of 17 bivalents at meiosis supports the morphological evidence that these 2 species are quite closely related. *Verbesina aristata* occurs in southern Georgia and Alabama and in northern Florida, especially in the panhandle region. *Verbesina warei* is endemic to the litoral of the central panhandle region of Florida. Although the ranges of the 2 species are contiguous, ecological isolation is evidently complete and the ranges apparently do not overlap. As would therefore be expected, an examination of herbarium specimens revealed no evidence of natural hybridization.

Intersectional crosses: Nine species from 5 sections were utilized in intersectional crosses. Each of the 4 successful crosses was between species of sects. *Pterophyton* and *Verbesinaria*.

Seeds from the cross *V. aristata (Pterophyton)* × *V. occidentalis (Verbesinaria)* germinated readily to produce robust hybrids. The leaves of the hybrids were intermediate between the petiolate, ovate ones of the male parent and the sessile, oblong ones of the female parent. The wingless stem of *V. aristata* dominated the winged condition found in *V. occidentalis*. The styliferous ray florets of *V. occidentalis* dominated the neutral ones of *V. aristata*. As might be expected for intersectional hybrids, meiosis revealed 34 univalents and pollen stainability was an

accordingly low 5%. Although the species are sympatric, no hybrids were detected in the herbarium material examined.

The cross *V. alternifolia (Verbesinaria)* × *V. aristata (Petrophyton)* resulted in a single seed which germinated to produce an initially weak individual. Vegetative morphological characters indicated this plant to be a hybrid. Like the male parent, it possessed wingless stems and the leaves were completely sessile and opposite rather than attenuate-based and alternate as in the female parent. Unfortunately this plant was inadvertently destroyed before material was taken for cytological examination. However pollen stainability was checked and found to be 4%. The low pollen stainability indicates a lack of chromosome pairing and further substantiates the hybrid nature of this individual. The species are sympatric, but no hybrids were encountered in the herbarium material examined.

The hybrids produced by the cross *V. warei (Pterophyton)* × *V. occidentalis (Verbesinaria)* possessed the wingless stems of the female plant and had leaves intermediate between the elliptic-oblong ones of the female parent and the larger, ovate or lanceolate ones of the male parent. The hybrid manifested none of the laxness of stems displayed by *V. warei*. Pollen stainability ranged from 1-4.5% and 34 univalents were observed at meiosis. No indication of natural hybridization was detected in an examination of herbarium material.

Seeds from the cross *V. rothrockii (Pterophyton)* × *V. longifolia (Verbesinaria)* germinated readily to produce both selfs and hybrids. *Verbesina rothrockii* has lanceolate leaves which are mostly opposite below but soon become alternate whereas the linear leaves of *V. longifolia* are frequently subopposite, subwhorled and alternate on the same plant. The hybrids had leaves intermediate in shape which were mostly opposite, the uppermost becoming alternate and possessed linear phyllaries such as are found in *V. longifolia* rather than oblong ones as occur in *V. rothrockii*. Meiosis of the hybrids revealed 17 bivalents with no abnormalities. Pollen stainability was correspondingly high,

ranging from 48-60%. Although the species are sympatric in southeastern Arizona, no natural hybrids were detected in the herbarium material examined.

CONCLUSIONS

The crossing program here reported involves too small a portion of the genus to permit broad generalizations. However some conclusions are in order. Although Robinson and Greenman (1899) retained *V. alternifolia* in the genus *Actinomeris*, there has been a tendency in recent years to treat this small genus of 2 species in *Verbesina*. The morphological characters, divergent pappus awns and globose receptacles, by which it is kept apart from *Verbesina* are weak. That an apparent hybrid was obtained between *V. alternifolia* and *V. aristata* further supports the morphological evidence that there is no justification for maintaining the genus *Actinomeris*.

The ease with which hybrids were obtained between sections *Verbesinaria* and *Pterophyton* suggests an affinity on the part of some of the members of these sections. The low pollen stainability and the lack of chromosome pairing in 3 of these successful intersectional crosses does not indicate a particularly close relationship. However the high pollen stainability and the occurrence of 17 bivalents with no abnormalities in the hybrids of the cross *V. rothrockii* × *V. longifolia* indicates a low genetic isolation and suggests the possibility that *V. longifolia* and its relatives may be closely related to some members of sect. *Pterophyton*. This also appears possible on morphological grounds. Robinson and Greenman considered sect. *Verbesinaria* to be unnatural, an opinion with which I concur. Additional crosses may be of aid in understanding the relationships of the species of this section. Since only sects. *Pterophyton* and *Verbesinaria* were represented by more than a single species in the crossing program, the failure to secure hybrids between other sections can not be taken as indicating that genetic isolation is complete between these sections.

DEPARTMENT OF BOTANY
UNIVERSITY OF GEORGIA, ATHENS

Table 1

MATERIAL USED IN CYTOLOGICAL AND CROSSING STUDIES

Species	Section	n =	Source
alternifolia (L.) Britt.	Verbesinaria	34	Bloomington, Monroe Co., Ind. *V6132*
aristata (Ell.) Heller	Pterophyton	17[a]	Lloyd, Jefferson Co., Fla. *V6123*
encelioides (Cav.) Benth. & Hook. f.	Ximenesia	17	Bisbee, Cochise Co., Ariz. *V6219*
encelioides (Cav.) Benth. & Hook. f.	Ximenesia	17	Floresville, Wilson Co., Tex. *V6117*
lindenii (Sch. Bip.) Blake	Saubenetia	17	Isthmus of Tehuantepec, Mexico. *V6138*
longifolia (A. Gray) A. Gray	Verbesinaria	17[a]	Ft. Huachuca, Cochise Co., Ariz. *V6135*
occidentalis (L.) Walt.	Verbesinaria	17	Whitehall, Clark Co., Ga. *V6210*
oligocephala Johnston	Sonoricola	17	Puerto Escondido, Baja California, Mexico. *V6233*
rothrockii Rob. & Greenm.	Pterophyton	17[a]	Mule Mountains, Cochise Co., Ariz. *V6133*
serrata Cav.	Saubenetia	17	Queretaro, Queretaro, Mexico. *144*
virginica L.	Ochractinia	17[a]	Tallahassee, Leon Co., Fla. *V6131*
warei (Nutt.) A. Gray	Pterophyton	17	Wewahitchka, Gulf Co., Fla. *V6130*

[a]Previously unreported counts

Table 2 CROSSING PROGRAM

Crosses	Total Attempts (florets)	% Seed Set	Comments
alternifolia × aristata	174	0.6	probable hybrid
× occidentalis	144	0.0	
× virginica	41	0.0	
× warei	81	0.0	
aristata × alternifolia	165	4.8	apparent self
× occidentalis	169	40.2	hybrids
× rothrockii	199	0.0	
× virginica	109	0.0	
× warei	65	29.2	probable hybrids
encelioides × oligocephala	207	0.0	
× virginica	190	0.0	
longifolia × rothrockii	111	8.8	no germination
occidentalis × alternifolia	101	11.9	selfs
× virginica	309	16.5	probable selfs
oligocephala × encelioides	33	0.0	
× rothrockii	55	47.3	selfs
rothrockii × aristata	90	0.0	
× encelioides	110	0.0	
× longifolia	196	15.6	selfs and hybrids
× occidentalis	77	0.0	
× warei	85	4.7	no germination
Virginica × encelioides	108	0.0	
× occidentalis	492	2.7	probable selfs
× oligocephala	120	0.0	
warei × alternifolia	28	0.0	
× aristata	55	25.5	hybrids
× rothrockii	23	0.0	
× occidentalis	58	12.1	hybrids
× virginica	64	0.0	

Table 3

ANALSIS OF HYBRIDS

Cross	Pollen Stainability %			Meiosis	
	Range	Average	No. Plants	Pairing	No. Plants
alternifolia × aristata	—	4	1	——	0
aristata × occidentalis	—	5	1	34 I	1
rothrockii × longifolia	48-60	53	3	17 II	2
warei × aristata	50-69	62	6	17 II	1
warei × occidentalis	1-5	2	2	34 I	1

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NEW RECORDS OF DISJUNCT ARCTIC-ALPINE PLANTS IN MONTANA

S. A. BAMBERG[1] AND R. H. PEMBLE[2]

Two recent studies dealing with Montana alpine vegetation (Bamberg, 1964; Pemble, 1965) have produced new records as well as significant range extensions for several species representing a major floristic element in the alpine flora of the state, namely the arctic-alpine element. Four of these species which fill gaps in previously reported distributions are: *Festuca baffinensis* N. Polun., *Juncus albescens* (Lange) Fern., *Juncus biglumis* L., and *Kobresia myosuroides* (Vill.) Fiori & Paol. Three other northern species have their southern limits in the Rocky Mountains within Montana. These are: *Cassiope tetragona* (L.) D. Don, *Dryas integrifolia* Vahl, and *Festuca vivipara* (L.) Sm.

FESTUCA BAFFINENSIS N. Polun. probably has a circumpolar distribution (Holmen, 1964) though Tolmachev (1964) does not believe that any of the Eurasian Arctic material can clearly be referred to a taxon separate from *F. brachyphylla.* In the Arctic *F. baffinensis* has a continuous distribution from Alaska across Canada to northeast Greenland, preferring areas with calcareous soil. It has also been recorded from Svalbard and Novaya Zemlaya (Holmen, 1964). The species is known from isolated stations in the Rocky Mountains as far south as Colorado (Weber, 1961) and Wyoming (Johnson, 1962). Hultén (1962) suggests the probable presence of the species in northwest Montana although no specific stations are indicated from the state. Our collections were made in Glacier

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[1]Present address: Desert Research Institute, University of Nevada, Reno.

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National Park, one at Siyeh Pass (8 Aug. 1964, *Harvey & Pemble 7135*, MONTU) and one on Mt. Henry (15 Aug. 1964, *Pemble & Harvey 128*, MONTU).

JUNCUS ALBESCENS (Lange) Fern. is regarded by Hultén (1962) as a Greenland-American, eastern Asiatic race of the circumpolar-montane *J. triglumis* L. Polunin (1959) indicates that *J. triglumis* and *J. albescens* form a circumpolar series, hybridizing where their ranges overlap. *J. albescens* has been reported from Wyoming (Johnson, 1962) and Colorado (Harrington, 1954). *J. triglumis* has been reported from New Mexico (Wooton & Standley, 1915) and from Utah (Tidestrom ,1925) although these early reports should be referred to *J. albescens* according to Fernald (1924). An early collection referred to *J. triglumis* was made in northwestern Montana and reported by Rydberg (1900). The occurrence of *J. albescens (J. triglumis)*, previously suspected in Montana (Booth, 1950), is confirmed by two collections made in Glacier National Park, one at Siyeh Pass (3 Aug. 1963, *Bamberg 825*, COLO), and a second at Logan Pass (2 Aug. 1960, *Schofield*, MONTU *51409*).

JUNCUS BIGLUMIS L. is considered by Polunin (1959) and Hultén (1962) to be a fully circumpolar species. Hultén's distribution map for the species shows disjunct stations in Colorado, where the species was reported by Weber (1955), and near the Beartooth Plateau in Wyoming. Two Montana collections of this species have been seen, both from Logan Pass in Glacier National Park (2 Aug. 1960, W. B. Schofield, MONTU *51397* and 21 Aug. 1962, *F. J. Hermann 18123*, MONTU). This species has not previously been reported for the state but Dr. F. J. Hermann has given us permission to publish the report of his collection from Glacier Park.

KOBRESIA MYOSUROIDES (Vill.) Fiori & Paol [*K. bellardii* (All.) Degl.] is considered by Hultén (1962) to be circumpolar arctic-montane species with a continuous distribution from the North American Arctic south to the international border. From there the species is disjunct with stations in the Wallowa Mountains of Oregon (Peck, 1961), the Beartooth Mountains of northwest Wyoming (Johnson ,1962),

Colorado where it occurs on scattered peaks (Harrington, 1954), Utah in the Unita Mountains (cf. Major & Bamberg, 1963) and New Mexico (Wooton & Standley, 1915). In addition, Major and Bamberg (1963) have reported its occurrence at Convict Creek in the Sierra Nevada of California where it is found with four other disjunct cordilleran species. Our collections are from Glacier National Park (3 Aug. 1963, *Bamberg 797*, COLO) where the species occurs at Siyeh Pass.

CASSIOPE TETRAGONA (L.) D. Don is probably circumpolar, being abundant almost everywhere in the Arctic except towards the highest latitudes (Polunin, 1959). The species has been reported as far south as Okanogan Co., Washington on the Pacific Coast and Glacier National Park in the Rocky Mountains (Hitchcock *et el.*, 1959). Our collection of the species (27 Aug. 1965, *Pemble 254*, MONTU) was made on St. Mary Peak in the Bitterroot Mountains of western Montana about 175 miles south of Glacier Park.

DRYAS INTEGRIFOLIA M. Vahl ranges throughout the Arctic regions of the western hemisphere from western Alaska to East Greenland (Polunin, 1959), across much of Canada south to southern British Columbia and Alberta and east to Newfoundland with an isolated station near Lake Superior (Hultén, 1959). This species has been reported once from Montana (Porsild, 1947) although Hitchcock *et al.* (1961) indicate that they have seen no material of *D. integrifolia* from the state. As the determinations of our *Dryas* specimens were made by E. Hultén we are including the collections from the Big Snowy Range *(Bamberg 313, 565, 769*, COLO) and from the Tobacco Root Mountians *(Bamberg 429*, COLO) which he referred to *D. integrifolia* ssp. *integrifolia* as confirmation of the species' presence in the state.

FESTUCA VIVIPARA (L.) Sm. is considered by Hultén (1958) to be a doubtful taxon with an uncertain geographical range. Its taxonomic status in the Eurasian Arctic has been questioned by Tolmachev (1964) who indicates that vivipary occurs in almost sporadic fashion throughout the area of *F. brachyphylla* and *F. ovina*. Hultén's distribution

map for the species shows it to be common in the Scandinavian mountains, in south Greenland, and in Iceland. He also cites reports from Novaya Zemlaya and other places in Arctic Russia. Fernald (1950) considers it to reach from Greenland and Labrador to Alaska and south to west Newfoundland, Anticosti, Gaspé Peninsula and Lake Mistassini, Quebec. Holmen (1964) indicates that *F. vivipara* (L.) Sm. is, in the sense of most authors, a complex probably consisting of a number of species and hybrids. Different chromosome races are known to occur although the taxonomic status of these has not as yet been determined. He suggests on the basis of chromosome number ($2n = 28$) that the typical race includes the taxon common in the Scandinavian mountains, in Iceland, and South Greenland, and that the viviparous *Festuca* with higher chromosome numbers, occurring in other parts of the Arctic, is probably closer to *F. brachyphylla* or *F. baffinensis*. Johnson and Viereck (1962) have indicated that their material from Alaska should be referred to the same taxon as that in Scandinavia. We also feel that our collections may be referred to the Scandinavian populations on the basis of external morphology, but we have made no chromosome counts. Several collections of this species have been made from Glacier National Park including localities at Logan Pass (11 Aug. 1949, *L. H. Harvey 4030;* 2 Aug. 1960, *Schofield,* MONTU *51406;* 8 Aug. 1964, *Harvey & Pemble 7091,* MONTU) and Siyeh Pass (3 Aug. 1963, *Bamberg 819,* COLO; 8 Aug. 1964, *Harvey & Pemble 7145,* MONTU). These stations are considerably removed from the range shown by Hultén (1958) for the species in which the Alaskan stations are not included. If the Alaskan reports are included the gap extends from Alaska to the area of our present report in Glacier Park.

In addition to the seven species just discussed which belong to the Arctic flora two other extensions of alpine species are worth reporting here. *Carex stenochlaena* (Holm) Mack., previously known from Alberta and Alaska south to Washington and Idaho, was collected at Logan Pass in

Glacier National Park by F. J. Hermann (26 Aug. 1962, *F. J. Hermann 18300*, MONTU) who has given us permission to include it as a new Montana record. A second interesting range extension is that of *Saxifraga tolmiei* T. & G. which is a typical member of the Pacific Coast-Cascade flora. This species was previously known in Montana only from St. Mary Peak in the Bitterroot Mountains although it is distributed along the Pacific Coast from Alaska south through the Cascades and Sierra Nevada of California (Hitchcock *et al.*, 1961). Additional Montana collections of this species were made on Trapper Peak (25 July 1964), *Pemble & Harvey 58*, MONTU), a southern extension of 50 miles, and in the Highland Mountains south of Butte, Montana, an eastern extension of approximately 80 miles.

Disjunctions, which are common in Arctic and alpine plant species, are of interest to those concerned with the floristic history of any region. Such disjunctions may also have environmental causes. The disjunctions we have noted suggest a discussion of some recent phytogeographical work along these lines.

Weber (1949, 1959, 1965) proposes that in the southern Rocky Mountains the richest alpine communities in terms of the Arctic relicts that they harbor are found in the most mesic areas, particularly where high ranges trending east-west lie between or connect the principal north-south ranges. In such ranges diurnal insolation through the summer months is less direct or of shorter duration, resulting in small bogs and lakes at high elevations. He indicates that the rare species may occur on either north- or south-facing slopes as well as in cold-air drainage basins. Johnson (1962) suggests that the disjunct occurrences of thirteen species in the Beartooth Mountains of Wyoming may be attributed to one of two factors: (1) that the bog environments are capable of dissipating the excessive summer heat allowing certain arctic-alpine relicts to persist, (2) that other arctic-alpine species can persist in the unstable environment of solifluction slopes. Dahl (1952, 1955) has pointed out that in Scandinavia the isotherms of the average yearly maxi-

mum summer temperature at the highest points of the landscape coincide closely with the distribution limits of a large number of arctic-alpine species. The importance of temperature is difficult to analyze in the Rocky Mountain alpine areas where high altitude weather stations and climatic data are scanty.

Fernald (1907) regarded the southern distribution of alpine species in eastern North America to be a function of the amount of calcium or potassium in the soil. In criticizing the "nunatak theory" later proposed by Fernald (1925), Wynne-Edwards (1937, 1939) suggested that most isolated occurrences could be better correlated with soils, particularly those rich in lime or combinations of magnesium, lime and soda, than with the presence or absence of Wisconsin glaciation in a particular area. Rune (1953) has proposed that the main soil factor involved in the distribution of alpine plants in Scandinavia appears to be the degree to which the humus colloids are saturated with cations, predominantly calcium ions.

In Montana, five of the seven arctic-alpine disjuncts occur in Glacier National Park on substrates derived from limestone and argillites of the Belt Series. This produces a clayey soil high in calcium. *Dryas integrifolia* in the Tobacco Root Mountains also occurs on mixed metamorphics where lime is present. *Cassiope tetragona* which was collected in the Bitterroot Mountains occupied a depressional area where snow often persists late into the summer, however the nature of the substrate was not determined. Intrusive igneous rocks predominate in the area although the possibility of a limestone outcropping is not ruled out. Tentatively we would say that the species has persisted in this locality due to conditions of the habitat such as those described by Weber (1949, 1959, 1965).

Langenheim (1962) reports the occurrence of populations of certain disjunct arctic-alpine species in Colorado on metamorphosed limestones along a contact of intrusive igneous rocks while others occurred along a contact between metamorphosed sediments of siltstone. Major and Bamberg

(1963) found disjunct species in the Sierra Nevada of California occurring on soils derived from calcareous parent material in conjunction with non-calcareous metamorphics. However, they also point out the presence of other smaller areas of calcareous metamorphic rocks in the Sierra Nevada where none of the disjunct species have been found, suggesting that there is no one-to-one correspondence here between edaphic specialization and floristic distinctiveness. They also point out the fact that their disjunct species are indifferent outside of the Sierra Nevada as far as calcicoly is concerned. According to Bamberg (1964), and as the work of Mooney & Billings (1961) confirms, many of the wide-ranging arctic-alpine species have northern and southern ecotypes.

In reviewing the literature dealing with disjunct or relict populations of arctic-alpine species it becomes obvious that such distributions cannot be attributed to any one factor. First, it is necessary to classify disjunct species as to their ecology throughout their continuous range of distribution as well as in the disjunct locality. We can then see how a population of *Festuca baffinensis*, found in open wind-swept areas in the Arctic, might persist in similar alpine situations, while such a locality does not harbor species of considerably different ecological requirements such as *Cassiope tetragona*, normally restricted in the Arctic to areas of snow accumulation. With this in mind we can next consider climatic limitations or edaphic specialization noting, for example, that soils high in calcium, or calcium and clay, such as the Montana localities previously discussed, are in fact often correlated with disjunct arctic-alpine species provided the first criteria is satisfied. It is also not unexpected that other relict species are found where contact areas in the substrate provide a unique edaphic situation satisfying the nutrient requirements of the relict species persisting there.

Gankin and Major (1964) have reviewed the problem of disjunct populations, and suggested that their presence may often be attributed to limited competition resulting from failure of the local, zonal vegetation to fully occupy the site.

This in turn is often correlated with an unusual edaphic situation. Contrary to this observation are our disjunctions of *Festuca baffinensis* or *Cassiope tetragona*. The former occurs on open sites in Glacier Park as well as in Colorado (Weber, 1961) where competition from zonal vegetation is not a factor while the latter occurs intermixed with a luxuriant growth of zonal vegetation, *Cassiope mertensiana*, suggesting that it is not limited to the relict site by competition. It is suggested that while a correlation between disjunct or relict populations and local vegetation in an azonal state may exist at lower elevations, such a relationship does not necessarily apply to all alpine situations where Arctic relicts occur.

Climatic conditions may be of importance directly, such as prohibitive maximum summer temperatures as suggested by Dahl and Johnson, or indirectly as they have modified a potentially suitable relict habitat. Thus, in analyzing disjunct and relict situations we should be prepared to correlate the presence of the disjunct relict species not with one but with several factors of the ecosystem which may interact and thus provide the necessary habitat suitable for its persistence.

DEPARTMENT OF BOTANY,
UNIVERSITY OF CALIFORNIA, DAVIS 95616

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DE PLANTIS TOXICARIIS E MUNDO NOVO TROPICALE COMMENTATIONES II

THE VEGETAL INGREDIENTS OF THE MYRISTICACEOUS SNUFFS OF THE NORTHWEST AMAZON

RICHARD EVANS SCHULTES[1] and BO HOLMSTEDT[2]

I.

The botanical sources of the sundry intoxicating snuffs of the New World tropics has long been uncertain or, in some instances, unknown. One of the most recently identified snuffs, prepared from the resin of various species of the myristicaceous genus *Virola* and employed by a number of Indian tribes in the northwestern part of the Amazon, is now relatively well understood as a result of interdisciplinary investigations of the past thirteen years.

It seems to be an appropriate time to appraise and integrate the numerous reports concerning the botanical ingredients of the myristicaceous snuffs and to summarize what we now know about this problem. It would appear, furthermore, an advantageous opportunity to offer such a summary, in view of current interest in the phytochemistry and pharmacology of the resin of *Virola* and related genera.

This paper is the second in a series dedicated to the study of poisonous plants of the New World tropics. The first paper in this series was published in the *Botanical Museum Leaflets, Harvard University* 21 (1967) 265-284.[3]

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[1]Botanical Museum of Harvard University, Cambridge, Massachusetts.

[2]Karolinska Institutet, Stockholm, Sweden.

[3]Part of the research reported in this paper was supported by the National Science Foundation through the R. V. Alpha Helix of the Scripps Oceanographic Institute in La Jolla, California. The authors were invited to participate in Phase C. of the Alpha Helix Amazon Expedition in 1967, under the direction of Prof. Carroll M. Williams of Harvard University. During July and August, we were able, as members of this team, to devote special attention to the myristicaceous snuffs of several groups of Waiká Indians of the Brazilian territory north of the Rio Negro. We were able, also, to begin phytochemical

II.

The sources of narcotic snuffs employed by natives of South America have long been clouded in mystery. It has been too widely assumed that all such snuffs were prepared either of tobacco or of *Anadenanthera peregrina*, more commonly known as *Piptadenia peregrina*. Reference to Cooper's map (7) purporting to show the distribution of the snuffing of *Anadenanthera* powder convinces the investiga-

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examination of a number of species of *Virola* and related genera. Our studies on the snuffs encompassed botanical, ethnobotanical, phytochemical and toxicological investigations and, viewed and interpreted against a background of what has previously been done, seem to lay a foundation for more intensive and extensive research along sundry avenues. Having the excellent laboratory facilities of this ship so near the scene of our field studies made it possible to carry out chemical observations that might have been out of the question in laboratories as far away as Europe or the United States. Detailed results of the phytochemical investigations will be published in a subsequent paper.

Part of the research was supported by grant MH-12007 (Holmstedt) from the National Institutes of Mental Health and by grant LM-GM 00071-01 (Schultes) from the National Institutes of Health. The drawings prepared for this paper have been executed through a grant from the Milton Fund of Harvard University.

We deeply appreciate the interest and help of our colleague, Commander Manoel de Oliveira Pérez of the Instituto de Pesquisas da Marinha of Brazil, liaison officer of the Brazilian Navy assigned to the Alpha Helix. Commander Pérez not only took an active part in several of the phytochemical surveys that we carried out aboard the Alpha Helix, but we are certain that, without his assistance, it would have been much more difficult to secure permission from the officials of the government to visit the Waika groups.

Our gratitude must, likewise, be extended to the Instituto Nacional de Pesquisas da Amazônia in Manáos and its officials, especially to its director, Dr. Djalma Batista, and agronomist, Sr. Vivaldo Campbell de Araujo; to the Instituto Agronômico do Norte in Belém do Pará, especially to Dr. João Murça Pires.

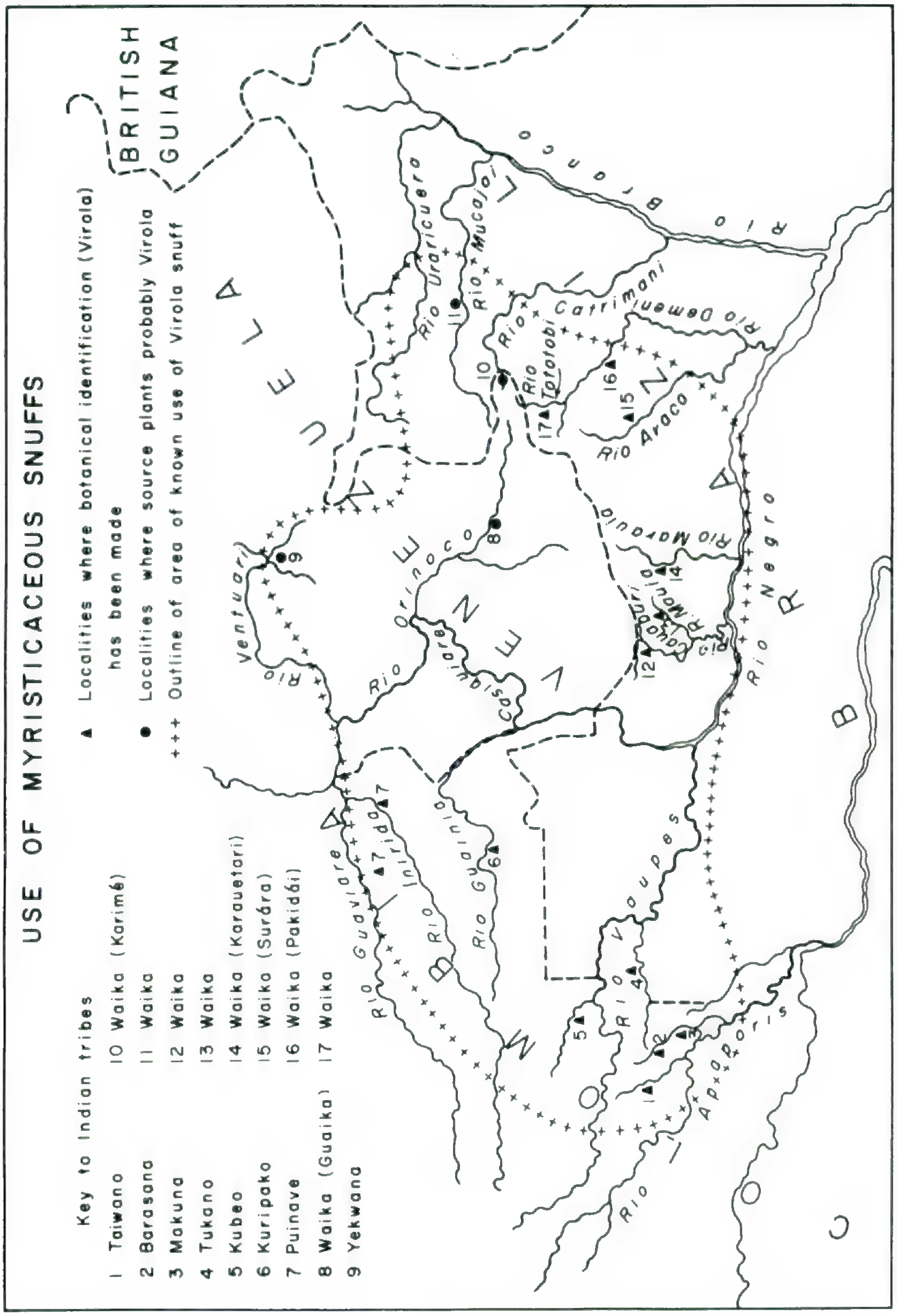
It is, furthermore, a pleasure to thank our good friends Padres José and Francisco of the Salesian Mission at Maturacá on the Rio Cauaburí and the Rev. Keith Wardlaw and Sr. Francisco Becerra de Lima of the New Tribes Mission at Tototobí. We are deeply indebted to Mr. Eldon Larson, pilot for the Mission Aviation Fellowship in Boa Vista, Brazil, for his kindness in making available to us air mobility at critical periods in our field research.

tor how uncertain the total picture is at the present time. Even a superficial study of Wassén's meticulous six-page legend to his map (38) showing the distribution of snuffing in South America will indicate how complex and how poorly understood are the sources of these sundry narcotic powders. Suffice it to say here that 1) *Anadenanthera* is employed as the source of a narcotic snuff on a geographically much more limited scale than the literature references generally would indicate; and 2) there are still botanically unknown snuff preparations in use in several parts of South America (28).

To the best of our knowledge, references to the myristicaceous snuffs are all found in comparatively recent literature. The older reports of snuff from the northwestern part of the Amazon and the upper Orinoco seem to be referable either to tobacco or to the seeds of *Anadenanthera peregrina*. Humboldt, Spruce and other early travellers and explorers in this vast region appear never to have encountered the preparation of a snuff from the bark of a tree; this is an especially interesting circumstance in the case of Spruce who devoted much attention to myristicaceous trees and who actually described a number of new species in this family.

What seems to have been *Virola*-snuff was first noticed and reported by the famous German ethnologist Dr. Theodor Koch-Grünberg (15), who lived amongst and studied Indian tribes in the Rio Negro basin and the upper Orinoco during the early years of the present century. While Koch-Grünberg failed to specify the botanical source of the narcotic, there seems, in the light of later investigations, to be little doubt that he was reporting actually the manufacture of a snuff from *Virola*.

Writing of the Yekwaná (Yecuaná) tribe (Karib-speaking Indians related to the Makiritare) of the Río Ventuari in Venezuela, Koch-Grünberg made the following observations: "Of an especial magical importance are the cures, during which the witch-doctor inhales *hakúdufha*. This is a magical snuff used exclusively by the witch-doctors and


USE OF MYRISTICACEOUS SNUFFS
▲ Localities where botanical identification (Virola) has been made
● Localities where source plants probably Virola
+++ Outline of area of known use of Virola snuff
Key to Indian tribes
1 Taiwano
2 Barasana
3 Makuna
4 Tukano
5 Kubeo
6 Kuripako
7 Puinave
8 Waika (Guaika)
9 Yekwana
10 Waika (Karimé)
11 Waika
12 Waika
13 Waika
14 Waika (Karauetari)
15 Waika (Surára)
16 Waika (Pakidái)
17 Waika
BRITISH GUIANA
VENEZUELA
COLOMBIA
BRAZIL
Rio Branco
Rio Uraricuera
Rio Mucajai
Rio Catrimani
Rio Demeni
Rio Toototobi
Rio Araca
Rio Negro
Rio Marauiá
Rio Orinoco
Rio Ventuari
Rio Guaviare
Rio Inirida
Rio Guainia
Rio Vaupes
Rio Apaporis

prepared from the bark of a certain tree which, pounded up, is boiled in a small earthenware pot, until all the water has evaporated, and a sediment remains at the bottom of the pot. This sediment is toasted in the pot over a slight fire and is then finely powdered with the blade of a knife. Then the sorcerer blows a little of the powder through a reed *(kuratá)* into the air. Next he snuffs, whilst, with the same reed, he absorbs the powder into each nostril successively. The *hakúdufha* obviously has a strongly stimulating effect, for immediately the witch-doctor begins singing and yelling wildly, all the while pitching the upper part of his body backwards and forwards."

In connexion with this postulated identification of the Yekwana Indian bark-snuff as *Virola*, it should be borne in mind that Dr. John Wurdack (43), after field experience in the Río Ventuari in recent times, has written: "While Schultes believed, from Koch-Grünberg's description of a Ventuari narcotic, that *Virola* bark-exudate was used in the Ventuari drainage, we have found no such present-day evidence. Don Melisio Pérez of San Juan de Manapiare, who is the docent for Ventuari Indian lore, knows of no tribes in this drainage using bark-exudate." The Piaroa now inhabiting the same river do, according to Wurdack, prepare a snuff from beans of *Anadenanthera peregrina*. Living in a deeply forested area where *Anadenanthera peregrina* does not occur, these Indians make a long annual pilgrimage to secure seeds of this legume for snuff-making.

In 1961, Dr. Helmut Fuchs of Caracas carried out field studies in the upper Río Ventuari. He mentioned (40) two snuffs, one of which has definitely, through botanical specimens, been determined as *Anadenanthera peregrina*. Of particular interest here, however, is his confirmation of Koch-Grünberg's statement concerning *hakúdufha*. In a letter to Dr. Henry Wassén (October 24, 1961), Fuchs wrote: "The crushed bark of *ai'-yuka (Piptadenia peregrina?)* (in the Venezuelan vernacular called 'yopo') is known as *a'ku:duwha* in the powdered form. In addition, the fruits of another plant are likewise consumed with

a'ku:duwha, which, judging from explanation by Makiritare Indians, might also be a *Piptadenia*. There are, furthermore, two other plants employed in the elaboration of the snuff: a broad-leaved one *(ai'-yuku)*, the bark of which is ground up with the *a'ku:duwha*, and a small-leaved one (unknown to me), the fruit of which is crushed. These two plants are found only in the highest mountains, for which reason the natives could not, unfortunately, bring me specimens. I agree with you that it seems as though the designations *ai'-yuku* and *a'ku: duwha* have a generic meaning".

If these data be accurate, they appear to indicate — beyond the implication that these native terms are generic for snuffs — that the powdered bark, as well as the seeds or fruits, of *Anadenanthera peregrina* are employed.

Although the literature usually indicates that it is the bean of *Anadenanthera* that is employed in snuff-making, there would seem to be no chemical reason why the bark should not also be used since, like the seeds, it contains several psychoactive tryptamines (12). The possibility that *Anadenanthera*-bark may be so employed is a consideration that must constantly be borne in mind in our attempts at "identification" without botanical material of the plant sources of snuffs. One is likewise tempted to ask whether or not the broad-leaved plant described in Fuchs' letter might be a species of *Virola*.

The first definite association of a snuff with *Virola* was made in 1939 by the great Brazilian student of the Amazonian flora, Dr. Adolfo Ducke (8). In his monographic treatment of the Leguminosae of the Brazilian Amazon, Ducke wrote, in a footnote to a discussion of *Piptadenia peregrina*, that: "Martius and other writers attribute to this species the source of the narcotic *parica* employed by certain Amazonian Indians (the powder of the crushed seeds is inhaled through the nostrils). Notwithstanding, according to information which I obtained from the natives themselves in two localities in the upper Rio Negro, the *paricá*-powder comes from leaves of species of *Virola* of the Myristicaceae." All of the recent intensive research has not been able to

substantiate the statement that the leaves are used: all ethnobotanical field work and all recent reports of those who have observed the preparation of *Virola*-snuff coincide in indicating that the resin from the bark is the part of the tree employed by the natives.

When one of the writers (Schultes) first went into the northwestern Amazon in Colombia — a region where he carried out continual field work in botany and ethnobotany from 1941 to 1953 — he fully expected to meet with the extensive use of yopo snuff prepared from the beans of *Anadenanthera peregrina.* The anthropological literature quite generally ascribed all narcotic snuffs of the Amazon not obviously prepared from tobacco to this leguminous tree. Amongst many tribes of the Colombian Amazonas and Vaupes, he met with the use — often excessive use — of tobacco snuff and, in several tribes, of a snuff made from coca *(Erythroxylon Coca).* He never met with any snuff called yopo or niopo nor with a snuff prepared from beans of a tree; furthermore, he failed to encounter, wild or cultivated, a single tree of *Anadenanthera peregrina.*

During the course of explorations in the Río Apaporis in Amazonian Colombia in 1951 and 1952, Schultes had, as assistants, several Puinave Indians from the Río Inírida: The Inírida is the highest Colombian affluent of the Orinoco, and it represents an area where the floras of the Río Negro-Vaupés and the upper Orinoco floras blend. Consequently, the Puinave helpers, from whom he first learned of the myristicaceous snuff, were familiar with many of the plants found in the Apaporis basin. They indicated two species of *Virola* — *V. calophylla* Warburg and *V. calophylloidea* Markgraf — from the resin of which a highly intoxicating snuff, called *yá-kee* in the Puinave language, could be elaborated (21, 22, 23).

During 1951, the almost wholly uninhabited Río Apaporis was opened up at several points for tapping wild *Hevea* rubber, and natives from sundry tribes of the Colombian Vaupés and even from the Rio Uaupés of Brazil were transported into the area by air. Schultes had, consequently, an

unparalleled opportunity of studying the preparation of the narcotic by natives of tribes normally isolated from one another by great distances, and his field investigations disclosed that a number of tribes knew of *Virola*-snuff, the use of which was restricted to their witch-doctors: the Puinaves of the Río Inírida[4]; the Kuripako of the Río Guainía; the Kubeo of the Río Vaupés and Río Papurí; the Barasana and Makuna of the Río Piraparaná; and the Taiwano of the Río Kananarí. Reports indicated that its use was known amongst Indians, especially the Tukano, of the Rio Uaupés in Brazil, and indirect evidence placed it likewise amongst the several tribes living on the Rio Issana.

Virola-snuff is called *yá-kee* in Puinave, *yá-to* in Kuripako. Amongst the Tukano and linguistically related tribes, it is known as *pa-ree-ká*, a loan word from the Nheêngatú or Lingoa Geral, a Tupí-Guaraní language once widely spoken in the northwest Amazon, especially of Brazil; this is the term by which snuff from *Virola* and from *Anadenanthera* are known today by the civilized inhabitants of the Rio Uaupés — Rio Negro area of Brazil.

In the Colombian Vaupés — its westernmost area of use — *Virola*-snuff is prepared rather simply. Schultes saw it prepared by Puinave, Tukano, and Kuripako Indians, and descriptions of its preparation from members of the Kubeo, Barasana, and Makuna tribes indicated no appreciable deviation from the process. In all cases, the same species were pointed out as sources of the snuff, although the possibility that other species of the genus could be used was indicated.

[4]What almost certainly indicates the use of *Virola*-snuff by the Puinave of Laguna Negro on the lower Río Inírida in Colombia is a passing reference (19) to a snuff called *ya-to*, prepared frcm the inner bark of a vine known also as *ya-to*, resembling *yasé* [yaje?], and the ashes of a tree called *matuire*. Both are boiled, then dried and pulverized. How much reliability can be placed upon the botanical statement that a vine is the source of the snuff is open to question. *Virola* species, of course, are all trees, never vines, but was the source plant actually observed or is this report merely the uncritical repetition of a native's statement? We can say, however, that the vernacular name of the snuff in Puinave is *ya-kee*, not *ya-to*, which is the term applied to *Virola*-snuff by the neighboring Kuripako Indians (22).

The Indians strip the bark from the trees usually in the early hours of the morning, before the sun has begun to penetrate the forest canopy to heat up the trunk. Large strips of the bark, which peels easily from the cambium, are torn from the trunk and tied into loose bundles. Almost immediately upon separation of the bark from the tree, a profuse exudation or "bleeding" of a thick reddish resin-like liquid, which soon becomes viscous, oozes forth from the inner surface of the bark in small drops. The active principle is contained in this exudation — called *oom* (latex), or, specifically referring to these species of *Virola*, *há-oom-tee-ĕt* or *yá-kee-oom*, in Puinave. According to the natives, this exudation is greatly reduced in quantity and is weaker in its narcotic effects when the trunk of the *Virola* tree has received the warmth of the sun's rays.

The bundles of bark are brought in and placed in water for about half an hour. They are then taken out, and the soft inner layer, on the surface of which the red exudation has congealed, is rasped off with a knife or machete. The shavings or raspings (*yá-kee-tao* in Puinave) are thrown into a large earthenware pot or enamel tray, and the rest of the bark is discarded. When enough shavings have been accumulated, a small amount of water is added, and the mass is thoroughly kneaded and squeezed by hand. The water becomes muddy and assumes a brownish or tan hue. This turbid liquid is strained several times, usually through a piece of finely hammered bark-cloth (prepared from *Olmedia* or *Poulsenia*), into a small-mouthed earthenware pot. The residual shavings, when as much of the water has been expressed as possible, are thrown away. Enough water is added to the strained liquid to fill the pot, which is then set to simmer over a slow fire. From time to time, a sordid foam, which rises to the surface, must be scraped off with a piece of bark. The boiling is allowed to continue for three or four hours, more water being added if evaporation is too rapid, until nothing remains except a thick, dark brown syrup at the bottom of the pot. This syrup must not be dried rapidly over a fire; the pot is set in the sun, and the syrup

is permitted to solidify slowly. When nothing but a dry, brown crust is left, the residue is scraped free from the pot and is ground into a fine powder with a water-smoothed stone as a pestle, and the pot or an enamelware tray as a mortar. It is then ready to be mixed with ashes which have been made from the bark of a small wild cacao tree (*Theobroma subincanum* Martius). Usually, equal amounts by volume of ashes and *ya-kee* powder are used. When they are thoroughly mixed, the product is put into a small bag made of finely hammered bark or cloth and is sifted through the bag by means of a gentle beating against the side of a small-mouthed receptacle. The resulting dust is the finished snuff. It is kept either in a small glass bottle, tightly corked, or else, more traditionally, in a type of jar made from a large snail-shell to which a hollow bird-bone tube has been fixed with pitch (usually from *Symphonia* spp. or *Moronobea* spp.). This tube is stoppered with a plug of feathers glued together with pitch at the basal end to form a tight-fitting stopper.

Amongst all the tribes of the Colombian Amazon, the consumption of *Virola*-snuff is limited to the medicine-men and is, therefore, small. Since it is said to lose its intoxicating properties rather rapidly, even when in a tight container, it is made in small amounts and frequently.

The next reference (2) to what seems to be the same myristicaceous snuff is found in an extraordinary article on the culture of certain Waiká Indians,[5] mainly those living

[5]In view of the extreme confusion in terminology in current anthropological literature and in line with a more popular usage of terms, we intend, for the ethnobotanical purposes of this study of snuffs, to employ the term *Waiká* generically for many groups of Indians, apparently closely related, who dwell in southernmost Venezuela and northwesternmost Brazil, in the headwaters of the Orinoco and on northern affluents of the Rio Negro, respectively. The final classification of peoples, naturally, lies with the anthropologist. Pending, however, a clearer classification for the area in question, specialists in other disciplines — such as ethnobotany — must have a simple nomenclature, and, consequently, we are faced with the necessity of choosing one for use in this paper, pleading the while for a more logical, meaningful and standardized treatment of what are obviously closely

related, sometimes even identical, peoples. Present knowledge of the snuffs of South America seems to support a suspicion that the Waiká (in our sense of this term) form the center of today's most intensive use of the myristicaceous snuffs and may even represent the area of origin of the use of these preparations. It is this consideration that has made imperative our search for a simple terminology for use in the present summary.

The Indians in question, who live in isolated hamlets or single communal *malocas*, are sometimes referred to inclusively as Yanonami, although the generic term Waiká is likewise very often employed to designate this large and dialectically somewhat heterogeneous group of natives. Actually, Waiká or variants of it represents the oldest term, having been first employed in the literature in 1779 (4). Some specialists have spoken of the Waiká and the Shirianá, although the name Shirianá (Xirianá) has also been used for groups in the Parima Mountain area of British Guiana and along the Ríos Uraricapará and Uraricoera in the uppermost Orinoco drainage-area. Koch-Grünberg (14) was apparently the first to conclude that the Waiká (Guaicá), Kirishaná, Guaharibo and Shirianá, all of the Parima region, were probably one group of people. Métraux (17) considered the Shirianá and the Waiká as distinct. Zerries (47, 49) referred to the Waiká, Guaharibo and Shirianá Indians, which apparently may form "an identical group inhabiting the headwaters of the Orinoco of Venezuela and adjacent parts of Brazil" and used Waiká for the entire group called Yanomamö by later workers. Becher (3), who employed the term Yanonami, distinguished several sub-groups living along the Rios Aracá and Demini, tributaries of the middle course of the Rio Negro, as the Surára and Pakidái. Seitz (31) followed Becher in considering the Waiká as belonging to the Yanonami or Yanoama, although one of the groups that he visited on the upper Rio Marauiá he called the Karauetari tribe. Salathé (20) referred to the Karimé, culturally related to the Waiká and living in the headwaters of the Rio Caterinani in Venezuela. Barker (2), a missionary with many years of experience with these several peoples in the upper Orinoco, stated that the ". . . Guaiká [Waiká] tribe inhabit the upper Orinoco and its tributaries . . . and also extends to Brazilian territory, occupying the headwaters of various affluents of the Rios Branco and Negro" and that the Waiká and Guaharibo ". . . speak the same language, but with dialectical differences." The Guaharibo, he reported, refer to themselves as the Shidishaná and Shirianá. Migliazza (18) did not accept Becher's inclusive use of Yanonami or Yanoama but preferred to speak of the "linguistic family Xirianá," living in a circular area the center of which is the Parima Mountain on the boundary of Brazil and Venezuela. They number, he stated, some 5000, divided into small groups of from 30 to 200 or more individuals; these groups, each generally with its own dialect, are

usually known as Shirianá, Waiká, Shamtari, Parahurí, Yanamani, etc. Wilbert (41), who has offered perhaps the most detailed treatment of the classification of these peoples, considers the Waiká as one sub-group of the Yanoama, suggesting that they are descended from very ancient inhabitants of South America. He considered the Surára-Pakidái (Sumatari or Samatari), Waiká, Karimé, Shirishaná (Casaparé), Warema (Sanema, Pubmatarí as all related and belonging to the Shirishana or Guaharibo family. Most recently, Chagnon (5, 6) has accepted the term Yanomamö for "... a tribe in Venezuela and Brazil who practice a slash-and-burn way of horticultural life," a term that the employed "in a linguistic-cultured sense to define the tribe. The word, he maintained, "means true human begins" since "their conception of themselves as the only true 'domestic beings' . . . is demonstrated by the contempt with which they treat non-Yanomamö who . . . are 'wild.' In addition to meaning 'people,' Yanomamö also refers to the language . . . Sub-Yanomamö groupings are based on language differences, historical separation and geographical location". We should point out parenthetically that tribal designations amongst South American Indians very commonly, in fact almost as a rule, mean only "human beings", "proper people", etc., to differentiate them from other linguistically non-accepted groups; it is not peculiar to the Waiká or Yanamamö. He asserted that "the Indians referred to themselves as Yanomamö, which at once defines their mode of life, language, origin and includes all people who share this mode of life, language and origin". He considered the Sanema, Shamatari and Waiká as "local groups". Two of these distinguishable groups, he pointed out, are the Waiká and Shamatari, both speaking nearly the same dialect but distinguished because of their separation and Shamatari "differentiation" from the Waiká in the past seventy-five years: those moving "to the south side of the Orinoco came to be called Shamataris by those living on the north side, and the term is now applied to any village in this area, whether or not it can trace its origin to the first supporters of Shamatari" (a kind of hero who, following intra-tribal fights, led his followers south to the Orinoco). Chagnon's map (5), shading in the Yanomamö area of southern Venezuela and northern Brazil, shows that his term is equivalent to what we prefer to call Waiká. He estimates their population to be up to 10,000, over 7,000 of them in Venezuela.

It may be significant that none of the several contributors to the *Handbook of South American Indians* (9, 13, 15, 16, 17, 32, 42) who have had occasion to refer to these Indians have employed the terms Yanamamö or Yanonami. They have used Waiká, often however distinguishing between the Waiká and the Shirianá.

These examples from the divergent opinions of the several anthropologically oriented specialists who have worked with and/or written about these Indians illustrate the dilemma that faces the botanist

near the mission station of El Platanal or Mahekodotedi on the uppermost Orinoco in Venezuela, not too distant from the area where Koch-Grünberg reported the bark snuff of the Yekwana tribe. In 1953, Barker, an American missionary with long experience in the region, offered a brief but telling sentence concerning the source of Waiká snuffs: "Different kinds of 'yopo,' of distinct strengths, are prepared from leaves, bark and ashes of bark." It should be noted that he made no mention of a *bean* or *seed*, thus, it would seem, ruling out the possibility that these people elaborated their snuff from *Anadenanthera peregrina.*

A year later, in 1954, the German anthropologist Dr. Otto Zerries (45, 46, 47, 48) began to publish a series of articles on the same and allied Indians: the Waiká of the village of Mahekodotedi and their relatives and neighbours whom he calls the Shi dishána of the Cantinama region of southern Venezuela. He wrote in great detail on the use and cultural significance of the narcotic snuff. His reference to the botanical sources of the snuff are, unfortunately, somewhat confused and often indecisive.

Zerries referred to "yopo-snuff" as "a characteristic feature of Waiká culture". This snuff, which the natives called *ebéna* and use "to be intoxicated and establish contact with the *hekula,* spirits of rocks and waterfalls", appeared "to be made of the seeds of *Mimosa acacioides* or of a *Piptadenia* species", a plant known to these Waiká as *hisioma.* Since Zerries worked with the same Indians on which Barker had based his report, one wonders, in view of Barker's explicit enumeration of "leaves, bark and ashes of bark" and his omission of "seeds", whether Zerries actually observed the use of *seeds.* By Zerries' acceptance of Cooper's distribution map detailing the use of *Anadenanthera (Piptadenia) peregrina* for snuff, it would appear that realizing that in certain parts of the upper Orinoco drainage-area, *Anadenanthera* seeds formed the prime source of a narcotic snuff commonly called *yopo* or *paricá,*

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and pharmacologist. We trust that, under the circumstances, our course of action will be understood.

he may conveniently have extended this generalization to his own group of Waiká. It is quite apparent that Zerries' identifications were not based on voucher botanical specimens. A botanist, had there been material to submit to a plant taxonomist for determination, would most certainly have known that the binomial "*Mimosa acacioides*" is merely a synonym of *Piptadenia peregrina*. Consequently, by extrapolation, it seems wholly probable that this "identification" of the source of *ebéna* was neither made by a botanist nor based upon voucher specimens. In late papers, Zerries asserted that the "yopo" of these Waiká is prepared basically from this leguminous tree.

It may be interesting, if only to illustrate the complex role that these intoxicating plants play in Waiká philosophy, to quote more fully one of Zerries' discussions of certain ethno-botanical aspects of the sources of the narcotic snuff of the Waiká. "The snuffing of yopo-powder during which persons sitting in juxtaposition, snuff each other through a tube half a meter long, is an indispensable prerequisite for invoking the spirits, for only then can the *hekula* enter the medicine man's chest and allow him to see the spirits in his yopo-intoxication. Sometimes, he is overcome with the drug and his own imagination and, more or less, loses his senses. This may sometimes be immediately manifest in a kind of seizure by the spirit that has laid hold of him, so that the medicine man cannot be exorcised by his colleagues. Now and then, he loses consciousness, a condition that the Waika revealingly call by the word for 'dying'. This effect is produced presumably by the alkaloid of a plant resembling a *Mimosa*, *Piptadenia peregrina*, and which is one of the numerous vegetal ingredients of the snuff. The plant *hisioma*, . . . from which this ingredient of the *yopo*-powder comes, . . . is subordinate to two *hekula* spirits, the *ihamaliwa* and *kuhidiliwa*, the lords of the sloth and of an unknown bird, who had, in primeval times, allowed the soul of the *hisioma* to come down and thus create the plant itself . . . Another ingredient, *mashohara*, derived from a species of *Piperaceae*, is also called *yauardi-*

hena ('leaves of the forest spirit') . . . A further snuff powder which, unfortunately, cannot be botanically identified, is called *bolek-hena,* signifying 'leaves of the spirit of the dead'; this plant is subservient to *hayacowardi,* a female demon in the form of a wildcat . . . Whoever . . . is rubbed with this plant will always . . . be at the mercy of this female demon."

A most revealing statement in this regard was made by Zerries in 1954(44). In speaking of other ingredients of *ebéna,* he mentioned *masho-hara* or *yauardi-hena,* which he described as the leaves of a piperaceous plant cultivated in the garden plots for this purpose and a powder made from an unknown plant known as *bolek-hena* ("leaves of the death spirits"). "The strongest ingredient is *yacoana,* the inner bark of a wild tree, which is dried, often toasted. I presume," he wrote, "that it is a species of *Mimosa (Mimosa acacioides),* which contains an alkaloid." Here Zerries asserted that the strongest ingredient of the snuff is the inner bark of a wild tree, not a "seed". Notwithstanding his presumption that it is *Anadenanthera peregrina,* there can be little doubt that this "wild tree" is a *Virola:* the inner bark is the part of *Virola* that is employed, and *Virola* is called *nyakwana* in other Waiká groups.

There are several other considerations in connection with possible identification of the plant ingredients of the Waiká snuff. These Waikás are forest-dwelling Indians, and *Anadenanthera peregrina,* definitely not a jungle tree, is found characteristically in open semi-savannah country. Zerries' descriptions and photographs of the snuffing equipment, snuffing ritual and physical effects of the narcotic are, in every detail, identical with those observed for *Virola*-snuff in other groups of these same peoples.

Consequently, it is obvious that we are left with extreme uncertainty, insofar as the botany is concerned, by Zerries' writings on the snuff. There are several possibilities: 1) that the snuff is prepared from seeds of *Anadenanthera peregrina;* 2) that it is elaborated from the inner bark of a

species of *Virola;* 3) or that there are several kinds of snuffs made by the Waiká — one basically active because of *Anadenanthera*, the other, basically active because of *Virola*. In view of the later anthropological and botanical field work, we believe that the second possibility is the more probable and that the *ebéna* of these Orinoco Waiká is a myristicaceous snuff.

In 1960 the German anthropologist, Dr. Hans Becher (3), referred to the use of an intoxicating snuff, especially in connexion with adolescent initiation rites and endocannibalistic ceremonies, by the Surára and Pakidái living on northern affluents of the Rio Negro in Brazil. These groups employ only two narcotics: tobacco, used hedonistically; and *epéna*-snuff, used ceremonially. The narcotic *epéna*-snuff, he reported, is, like *yopo* or *paricá*, prepared from a number of ingredients. It is made, according to this reference, from the roasted and powdered *paricá* seeds *(Anadenanthera peregrina)* to which the ashes of the bark of a "wild species of *Mimosa*", *hekurahihena*, and the piperaceous *maxaraha* are added. He suggested that the wild mimosoid plant might be "*Mimosa acacioides*", apparently not realizing that this binomial is a botanical synonym for *Anadenanthera peregrina* or *Piptadenia peregrina*. In one point in his discussion, Becher equated the "piperaceous" *mazahara* with the *mashoraha* reported by Zerries from the Waiká of Venezuela. There is no indication that botanical specimens formed the basis of the identification of these plant sources, and one wonders whether or not Becher relied upon the identifications earlier published in Zerries' papers.

A recent popular article by Dr. Napoleon Chagnon (6) on the Waiká and related Shamatari failed to refer to the preparation of their snuff, mentioning the narcotic only in a caption under an illustration showing a group of Indians snuffing: "In preparation for duels, the Indians take their hallucinatory drug, *ebene* . . .". In his unpublished doctoral thesis Chagnon (5) likewise did not consider the snuff.

In 1960 Mr. George Seitz (29), who with his wife had, in 1957, visited a group of Waiká and others whom he calls

Shamatari and Araraibo on the Rio Maiá, a tributary of the Cauaburí, published a book on his trip to these people. He described the taking of snuff by these Waiká but, as he wrote, "as regards the powder snuff, we could find out nothing. He [the Indian] said that it was prepared from the bark of a shrub which grows only in the montains. His description, however, was so general that we could not identify the plant." Later, in a letter to Wassén (April 19, 1961), Seitz added significant data concerning the preparation of the snuff, called *epéna* by these people: "The snuff, the elaboration of which we saw more than once, consists of the following ingredients: 1) The bast of the bark of a tree (called *epéna-kési*). This bast is dried, toasted and then powdered. 2) The outermost bark of young stems of an *Acacia*-like plant (called *ama-asita*). It is dried completely and burnt to ashes (called *jupi-uschi*). An herb about 30 cm. tall (called *mashi-hiri*) is dried and powdered and mixed with both of the other ingredients." Subsequent to this letter, Seitz added even more data in several articles (30, 31) and has produced an excellent motion picture showing the preparation and use of *epéna*-snuff amongst the Waiká of the Rio Maturacá. This more recent information has been supported by botanical specimens that have been submitted to taxonomists for identification and prepared snuff-power that has been studied chemically and toxicologically (12). In 1965, Seitz (30) published observations on the use and effect of *epéna* in which he summarized what he then knew concerning the plant ingredients of the snuff. He recognized two different snuff preparations.

One was, as he had previously stated, prepared from three ingredients: 1) the bast of a tree; the small leaves of the herbaceous *mashi-hiri;* and the ashes of the outermost bark of an *Acacia*-like species called *ama-asita.* Botanical material of the first and apparently principal ingredient was identified by Dr. Eberhard Schmidt who ". . . came to the unequivocal conclusion that the specimen was *Virola,* fam. Myristicaceae. To my great content, I afterwards found the following statement: *Engler-Prantl,*

Die natürlichen Pflanzenfamilien, 2. Aufl., Band 17 a II, p. 193. The bark from *Virola calophylla* Warburg and *V. calophylloidea* Markgr. — gives a narcotic snuff powder *(yá-ka, yá-lo)* used by various Indian tribes in the Amazon region and in Colombia". Seitz did not offer botanical determinations for the second ingredient. The third, he remarked, resembled an *Acacia*.

We have had an opportunity of examining Seitz' botanical material. Some of it comprises small pieces of bark and twigs that do not lend themselves to easy or exact identification, but some of the specimens are very adequate. Of the principal ingredient, we have one twig *(Seitz 1b)* and several pieces of bark *(Seitz 1c)* collected on the Rio Marauiá. They seem definitely to be referable to the Myristicaceae. These specimens, together with a photograph of a sterile branch of the *epéna* plant, allow us to identify the principal ingredient as *Virola*. Seitz has identified it in his papers as *Virola calophylloidea*, but the photograph looks to us more like *V. theiodora*. He submitted no specimens of *mashi-hiri*, the second ingredient. Of the third plant, *ama-asita*, we have seen several small bark samples *(Seitz 1h)* and a small transverse section of a branch *(Seitz 1i)*, both of which are definitely leguminous; and a dried, pressed leaflet and a photograph of a branch, both of which we would refer to the genus *Elizabetha*.

Seitz (31) reported of *ama-asita* that it "is a tall tree . . . it seems to be a *Trichilia species* . . . and seems to be rare."

Powder prepared from these three ingredients was analyzed by one of the writers (Holmstedt), using both bioassay and conventional biochemical techniques, with especially significant results from gas chromatography (10). The main component is 5-methoxy-N, N-dimethyltryptamine, but smaller amounts of N, N-dimethyltryptamine and 5-hydroxy-N, N-dimethyltryptamine (bufotenine) were likewise found in it.

Amongst the Waiká in the Marauiá drainage-area, Seitz learned of several other ingredients of snuff, but nothing is

known of their botanical identification. "There is also used another snuff powder which contains, besides the above mentioned three ingredients, the other vegetables: 1) the leaves of a plant called *poschi-have-moschi-hena (hena* means 'leaf') ; 2) the leaves of another vegetable called *ai-amo-hena.* In the villages we visited, the Indians either could not or did not want to show us these two plants. They always said that they only grew in the higher region of the mountains and not nearby. For this reason, the powder compound of the five ingredients was not at hand. In my opinion, it is the same compound whose snuffing we saw in our first expedition and whose effect was described as noxious for health . . . I cannot at the moment say more about this powder. Neither the missionary with whom I am corresponding and who lives in continued contact with several tribes, nor myself, saw in our other expeditions a similar effect again, and in no other visited tribe were we able to get this powder."

There are, further, several very interesting and possibly significant Seitz collections from the Cachoeira Guirapajé on the Rio Marauiá. One *(Seitz 4b)* consists of a small piece of a branch of *Anadenanthera peregrina.* The other *(Seitz 4)* is a very adequate herbarium specimen in fruit of this same species. Excellent photographs of the tree from which these specimens came were published by Wassen (36) : one, an unmistakable trunk of *Anadenanthera peregrina* with the characteristic mammilose projections; the other, leaves and pods of the same tree. Seitz nowhere indicates that the Waiká employs this tree in preparing a snuff. His collections and photographs do, however, establish the presence in this part of the Rio Negro of *Anadenanthera peregrina.* This area is deeply and uninterruptedly forested, and *Anadenanthera peregrina* does not occur there naturally. It is obvious that these Waiká must have imported seeds of this tree from rather distant localities of semi-open savannah, such as parts of southern Venezuela or the Boa Vista area of the Rio Branco of Brazil, where *Anadenanthera peregrina* grows sponta-

neously. The question remains, nonetheless: why are these Rio Marauiá Waiká cultivating *Anadenanthera peregrina?*

Seitz (31) has given further valuable data on the myristicaceous snuffs. In the town of Tapurucuara, a large village on the main course of the Rio Negro above its confluence with the Rio Branco, Seitz witnessed the preparation of a snuff by a Tukano medicine-man originally from the Río Papurí on the Colombo-Brazilian boundary. This powder was called *paricá*. The medicine-man still used the snuff in his practice. In its preparation, according to Seitz, he employed: ". . . the same raw material as the Waiká Indians — the inner layer of the bark from *Virola calophylloidea* Markgraf, but he prepared the powder in a very different way".

Scraping off the inner layer of the bark, he cast the pieces into a pot of water, kneaded them and squeezed until the water was reddish brown and muddy. Then the liquid was evaporated over a slow fire. In several hours, there was a hard crust left; this was scraped off with a knife and ground finely with a smooth stone. This powder, without any further admixture, was the snuff.

We have examined four herbarium specimens collected by Seitz in Tapurucuara in August, 1965, as representing the species employed by the Tukano medicine-man as his source of *paricá*. They appear to us to represent, like the material gathered in the Waiká village on the Rio Marauiá,

Virola theiodora.

During the summer of 1967, we were able to pursue our studies of myristicaceous snuffs in two widely separated Waiká villages in the Rio Negro drainage area of Brazil: Maturacá, on the uppermost Rio Cauaburí, an affluent that enters the Negro above Tapurucuara and the rises in the Sierra Neblina land mass on the Venezuelan-Brazilian boundary; and Wayhana-oo-thle, a very small village on the Rio Tototobí, a headwaters tributary of the Rio Demini, a northern affluent that empties into the Negro slightly above the town of Barcellos.

Plate 1373. Foliage and flowers of *Virola theiodora*, Manáos, Brazil.

The natives at Maturacá are closely related to those contacted by Seitz on the Rio Marauiá, a river that parallels slightly to the east, the Cauaburí. Understandably, their method of preparing the snuff is very similar to that described by Seitz. The natives on the Tototobí, on the contrary, elaborate their snuff quite differently.

The Maturacá Waiká store *epéna* in a large bamboo tube hanging from the house beams, and it is employed by any adult male singly or in groups at any time as well as during festivals. The tube is kept full, and the snuff, consequently, is always available for use. Every now and then, an Indian

will take the snuff, become intoxicated, dance and sing all alone, with the rest of the village going about its usual chores and not paying any heed to him. As Seitz noted in the neighbouring Karauetarí village on the Rio Marauiá: ". . . there is no system for the snuff ceremony . . . . there were Indians who took *epéna*-powder every day at any time in the afternoon; there were others who practiced the ceremony only once in a fortnight. Seldom did we see any formal motive for taking the snuff, such as curing a sick person, invoking success in the hunt or thanksgiving for a successful hunt".

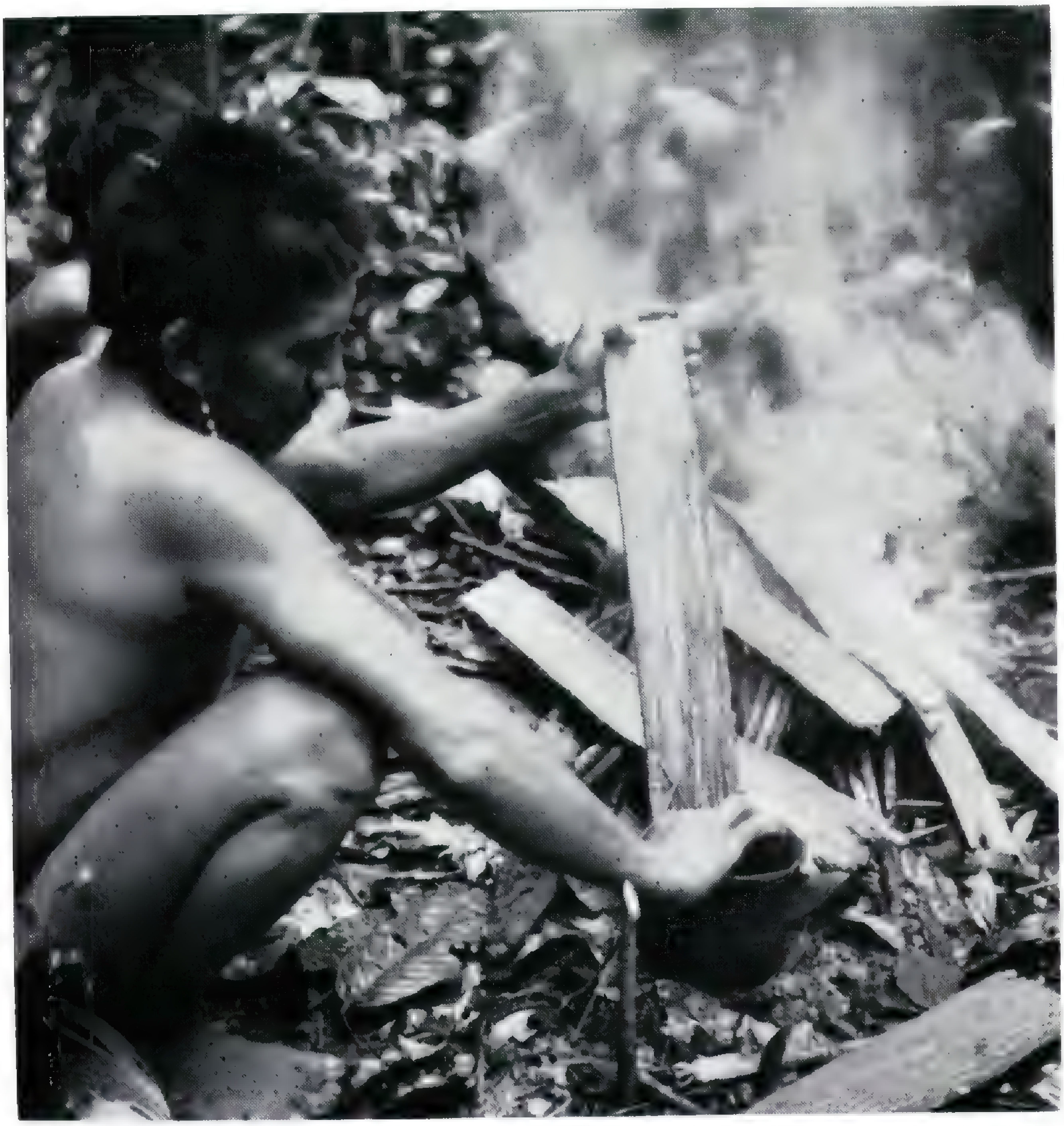


Plate 1374. Waiká Indian collecting resin from heated pieces of bark of *Virola theiodora*. Rio Tototobí, Brazil.

The ingredients of the *epéna*-snuff at Maturacá are three plants: *Virola theiodora, Justicia pectoralis* var. *stenophylla* and *Elibabetha princeps.*

Bark is stripped from trees of *Virola theiodora.* A young tree (height about forty feet, diameter fifteen inches) is preferred, although older and larger trees may be used. The natives assert that the yonger trees have a "stronger blood", but more probably the choice of the young tree is dictated by easier stripping of the bark. The strips are bundled and brought into the village. The soft, inner layer is carefully scraped off; the shavings are dried — first in the sun, then by gentle toasting over a slow fire — and stored until needed. When a new batch of snuff is to be made, these crisp shavings are pulverized by grinding them between the palms of the hands, the hands being held firmly between the knees while the grinding motion is in process. The ground shavings drop from the hands onto a banana leaf. The crudely ground shavings are collected from the leaf and placed in a hollow lecithydaceous fruit as a mortar *(Bertholettia excelsa* H. & B.) and triturated with a heavy wooden pestle until the material is almost completely pulverized. This powder is then sifted through a small basket to remove fibres, pieces of wood and other undesired refuse. The resulting powder is very fine, homogeneous, chocolate-brown and highly pungent.

Next, a powder of the leaves of a plant called *mashi-hiri* is prepared. This twelve- or fifteen-inch herb, cultivated in dense patches near the edge of the village, is the acanthaceous *Justicia pectoralis* var. *stenophylla.* It is kept hanging in bunches from the house-beams and is, consequently, usually quite dry when needed. The whole plant is crushed between the hands, the powder is sifted to remove bits of the stem and other refuse, and the resulting fine greenish dust is added to an equal amount of the brown *Virola*-powder. The *Justicia* plant is pleasingly aromatic as it hangs drying, and the prepared powder is even more highly aromatic. The natives assert that it is added to "improve the smell" of the final *epéna*-snuff and that it is

Plate 1375. *Justicia pectoralis* var. *sphenophylla* growing at the edge of a cultivated plot. Maturacá, Rio Cauaburí, Brazil.

not active. While it is true that other groups of Waiká prepare a potent *Virola*-snuff without the *Justicia*, preliminary chemical investigation of this acanthaceous plant suggests that we may be unwarranted in assuming that it is wholly inert ingredient devoid of pharmacological activity.

Seitz found that the Karauetarí did not add *mashi-hiri* to the snuff, whilst the Indians of the Marauiá did. He remarked of *mashi-hiri*, which undoubtedly is the same *Justicia* called *mashi-hiri* by the Waiká of Maturacá, that in "another Waiká village, near the Maturacá-channel, we saw that a third ingredient was added: the little leaves of a herbaceous plant, called *mashi-hiri*, like the *epéna*-scrap-

Plate 1376. *Justicia pectoralis* var. *sphenophylla* hanging to dry, together with a bamboo tube of *Virola*-snuff and the woven basket used to sift the prepared snuff. Maturacá, Rio Cauaburí, Brazil.

ings, dried and powdered. These leaves, however, have no intoxicating effect. The Indians say they are merely aromatic. I don't know why the Karauetarí didn't use the plant. Perhaps it was not available at the moment, or the Indians in the Marauriá River liked another flavour."

A number of years ago, a missionary working amongst the Waiká in the headwater regions of the Orinoco in Venezuela handed one of the authors (Schultes) a partially rotted, matted roll of plant material that he claimed to be the source of a narcotic snuff of these Indians (28). The condition of the material was very poor, and it disintegrated

Plate 1377. Waiká Indian about to grind to a fine powder crushed and dried leaf material of *Justicia pectoralis* var. *sphenophylla* for mixing with the powdered resin of *Virola* and ashes of *Elizabetha*. Maturacá, Rio Cauaburí, Brazil.

upon study, but it seemed to represent a species of *Justicia*, an identification that was corroborated by the late Dr. E. C. Leonard, specialist on the Acanthaceae. With the unsatisfactory preservation of the material, Schultes' inability to visit the region personally, and the failure of other botanists who had worked in the general area to report it, Schultes more or less dismissed *Justicia* as a serious contender for inclusion in our list of hallucinogenic plants. We now realize that it is definitely a common ingredient of the myristicaceous snuffs of the Waiká.

There is a further piece of field information that may now have a bearing upon this general topic. *Justicia pectoralis* var. *stenophylla* has been collected frequently, especially near cataracts, in the Río Apaporis drainage-area of Colombia. One of the collections (*Schultes & Cabrera 15244*) from the Río Pacoa, an affluent of the middle course of the Apaporis, bears an annotation that the name of the plant in Puinave is *ya-ka-yoó*. Since the Puinave name for *Virola*-snuff is *yá-kee*, one might well wonder if this similarity of native epithets could indicate some connexion in use of the *Virola* and the *Justicia*. Schultes never, with the numerous collections that he made of *Justicia pectoralis* var. *stenophylla*, was given any data that might suggest that Indians of the Colombian Amazon employed the plant as an admixture with *Virola*-resin. Yet the coincidental similarity between the names *yá-kee* and *ya-ka-yoó*, viewed in the light of what we know amongst the Waiká, is provocative of conjecture.

The third ingredient of the *epéna*-snuff of Maturacá is the ash of the bark of *Elizabetha princeps*, known in Maturacá by the Waiká name *a-má*. This tree is undoubtedly the same as that reported by Seitz as *ama-azita* on the Rio Marauiá. Bark is stripped from the trunk of this rather large and majestic tree. The inner, soft part of the bark is scraped off and thrown away. The hard grey outer bark is chopped into small pieces and set in a glowing fire. When they themselves begin to glow, they are removed, set aside and allowed to reduce to ashes. The ashes, which are nearly white, are carefully gathered up when cool, inspected critically for possible contamination in the form of sticks, bits of leaves or other extraneous material. The ashes that pass this inspection are then mixed, in approximately equal amounts with the *Virola-Justicia* powder. The resulting *epéna* snuff is greyish and extremely fine. We have every reason to believe that this ash may be an inert ingredient, although it may serve as a means of drying, to free the alkaloids more easily from the resin, to keep the snuff from deteriorating rapidly when stored in the

bamboo tubes, or merely for mechanical purposes.

The manufacture of the narcotic snuff amongst the Waiká of the Rio Tototobí is most interesting and very different from the methods described for other groups of these Indians. The resin of *Virola theiodora* is employed alone, without any admixture.

The bark of *Virola theiodora* is stripped first from the base of the tree with the tree standing, then, after felling, the entire trunk is stripped. As at Maturacá, relatively young trees are preferred. If more bark is needed for the batch of snuff required, additional trees are felled. Our visit, fortunately, coincided with the annual endocannibalistic festival and a large supply of snuff was needed: three trees were felled and completely stripped. The Tototobí Waiká, unlike the Maturacá group, apparently do not usually keep a large quantity of the snuff available at all times, nor is the use of the snuff, it appears, so frequent and casual.

The natives assert that the bark on the lower four or five feet of the trunk is richer in resin than higher up on the tree. When the lower bark is stripped and used, and prior to the felling of the tree, an Indian boy climbs to the top of the trunk, to the first main branch, with a circle of stout vines into which he has placed his feet. He then repeatedly slides down the trunk, scraping the bark vigourously with the vine-loop each time with his whole weight. This operation, they believe, causes the resin in the bark to "loosen" and, later, to flow more readily when the bark has been stripped from the tree. Occasionally this same scraping operation is carried out with the back of a machete before the lower bark is removed.

The pieces of bark that are stripped off measure two feet in length and five or six inches across. All of the preliminary preparation of the snuff is done in the forest where the tree is felled. A fire is made in the path, these strips are laid over the slow fire with the inner surface of the bark facing up. The gentle heating of the bark causes a very copious "bleeding" of the red resin, so copious that

Plate 1378. Pulverized dried resin of *Virola theiodora*, ready for use as snuff, together with an unground piece of the resin. Rio Tototobí, Brazil.

large drops flow together, and soon the inner surface of the bark is covered with the liquid. Then the Indian in charge of this operation picks up the strips, one by one, holding each piece vertically over a small clay pot. He lets the resin flow down and drop into the pot, running his index finger down the inner surface of the bark to scrape off every drop of the resin. The bark is once again laid over the fire and reheated. More resin appears. This is done several times before the Indian throws the bark away because the resin in it has been exhausted. A large number of these strips are treated in this way, unhurried care and meticulousness

marking the whole operation. The amount of resin extracted when we witnessed this work amounted to about two teacups full and was the result of "bleeding" three trees. One of the trees was about seventy feet in height and measured fourteen inches in diameter; the other two were smaller.

When enough resin has been gathered, the Indian gradually heats the pot, and the resin boils slowly and is allowed to boil until it becomes thick enough to carry back to the house without its slopping out of the pot during walking. By this time, most of it has, upon cooling, crystallized into a beautiful, bright amber-red resin. Once the Indians have returned to their house, the crystallized resin is scraped from the sides of the clay pot with a sharp-edged stone and is then pulverized finely by grinding the powder accumulated in the bottom of the pot with the same stone as a pestle. Once it is deemed sufficiently fine, the powder is removed and placed on a banana leaf. It is a light coffee colour. The native begins a meticulous scraping of the carbonized resinous material from the sides of the interior of the pot and the grinding, as before, of this very dark blackish brown powder until it, in turn, is deemed fine enough.

When the whole operation of grinding had begun, certain lumps of very thick resin that had not crystallized were removed from the pot and put onto a small stick. This stick was put over a fire and hardened, then pressed out on a heated surface over the fire and allowed to carbonize. The carbonized lump was then added to the similar blackish brown powder in the pot and completely reduced to a fine powder.

At this point, the first brown powder and the second blacking brown powder were united and fully mixed to prepare the final snuff. Either one of these two powders,

[5]The authors, in self-experimentation, inhaled the second, carbonized powder.

Plate 1379. Waiká Indians picking out stem material from *Justicia pectoralis* var. *sphenophylla* prior to drying the leaves for use in the *Virola*-snuff. Rio Tototobí, Brazil.

however, has the potency and may be used alone as snuff.[5] This snuff — as well as the tree from which the resin is extracted — is known by the Waiká of the Tototobí as *nya-kwá-na*[6].

At Tototobí, *nyakwána*-snuff is made usually without any admixture. Ashes are, according to our information, never

[6]Although we are not anthropologists, we feel constrained to call attention to the curious similarity between the name of a tribe and linguistic group of Karib-speaking Indians on the Río Ventuari in the uppermost Orinoco basin of Venezuela-Yekwana-and one of the Waiká names for the myristicaceous snuffs *nyakwána* (the other Waiká name being *epéna*). This may be coincidental, but it should be pointed out, so that linguistically oriented specialists may consider whether or not there may be any significance to this observation.

added. These people know and do cultivate *Justicia pectoralis* var. *stenophylla*, which they call *masha-hára-hanak* (*hanak* means "leaf"). There is another name for this *Justicia* at Tototobí: *boo-hanák*. The Indians know that it can be used as an aromatic mixed with the *Virola*-resin dust, and they very occasionally do use it in this way, but it is the exceptional, not the usual, method of preparing *nyakwána*-snuff.

Interestingly enough, the Tototobí people do not know the custom of mixing ashes of *Elizabetha* or of any other plant with the *Virola*-powder. What may be even more significant is that they do not use *Anadenanthera peregrina* in preparing a snuff. In fact, several of these Tototobí Waiká knew vaguely of the snuff made from seeds (*Anadenanthera peregrina*) amongst the Makiritare far to the north and northeast and affirmed that they themselves had never employed seeds or beans to make snuff. We saw no cultivated trees of *Anadenanthera peregrina* in or near their village, and they assured us that the tree was unknown in their area.

III.

There is still an extraordinary facet to this study of *Virola* amongst the Waiká — its use as the source of an arrow-poison. Salathé (20) reported that the Karimé, culturally and geographically close to the Waiká of the upper Orinoco region, use as a poison for hunting monkeys and birds ". . . *jakuana*, which is extracted from the bark of a tree"; the term *jakuana* is, obviously, related to if not the same as *nyakwana* employed for *Virola* by the Waiká of the Tototobí. In discussing the Waiká (Surára) of the Rio Arará, Becher (3) reported: "The third kind of arrow-poison is the weakest. It is prepared from the snuff powder *epéna* by mixing it with water and letting it boil. This method is likewise known to the Pakidái and Shirianá." Becher unfortunately could not witness the preparation of this poison. Since it seemed to be a closely guarded secret, his knowledge of it was only from hearsay.

This information is, ethnopharmacologically speaking,

extraordinary. It is the first time that *Virola* has been indicated as the basis of an arrow-poison. Since we could not understand what constituent of *Virola* might be responsible for the toxic effects when employed on arrows or darts, and realizing that Becher had not witnessed the actual preparation of the poison, we were constrained to suspect an error in ascribing the source to *Virola* or to its being the same tree from which the *epéna*-snuff was made.

During our visit with the Tototobí Indians, however, we fully substantiated Becher's statement. Arrows were poisoned with the resin from *Virola theiodora*. Furthermore, they were poisoned with resin from the very same trees from which the snuff was being made. And what is even more surprising, the arrows were poisoned without any prior preparation of the resin.

These Indians state that they use no other kind of arrow-poison than this *Virola-resin* which is called simply *nyakwána-hoó-soo (hoó-soo* meaning "latex" or "resin"). They know that other Waiká groups prepare arrow-poison "from a vine" and indicate (with hand motions) a large liana with roundish leaves and a stem diameter of eight or nine inches.[7]

The poisoning of arrows in the Tototobí group is interesting. During the operation in the forest of heating the pieces of stripped *Virola* bark and scraping off the warm resin into the clay pot, an Indian occupies himself solely with the poisoning of arrows. Running his index finger up and down the exposed trunk from which the bark has been stripped, he gathers the slime and paints bamboo arrow heads with it repeatedly. He then heats the arrow-heads slowly over the fire to liquefy the resin slightly, spreading it more evenly with his finger. The heads are slowly turned in the smoke of the fire. When they have cooled and the preliminary smearing has completely hardened, the Indian

[7]The Waiká at Maturach pointed out to Schultes several menispermaceous vines that they employ as the basis of their arrow-poisons.

Plate. 1380. Waiká Indian preparing arrow-points smeared with resin of *Virola theiodora*. Rio Tototobí, Brazil.

begins to apply pure resin to the tips — resin that he scrapes from the heated strips of bark or that he takes from the accumulation in the pot. There are twenty or thirty applications of resin to the arrow heads, each application followed by a slow heating in the smoke. Then, finally, our Indian wraps a knot of palm leaves around the top of a stick, inserting the arrow tips in this knot — like pins in a pin cushion — and sets the stick in the ground in the sun to dry slowly. This represents the whole process of poisoning arrows or darts, an exceedingly simple one compared to most of the elaborate curare preparations of South America.

It is significant to note that during the annual endo-cannibalistic festival, when these Waiká ran out of the snuff that they had prepared for the occasion, they took several bamboo tube cases, in which they had packed the newly prepared arrow tips, scraped the *Virola*-resin from the arrow points and used the resulting powder as snuff during the dance. It had the same effect as the snuff that they had been using and which had been exhausted, and, inasmuch as both the arrow-poison and the snuff had been prepared in almost identical procedures from the same trees, there is no reason why it should not be interchangeable.

We do not yet know which chemical substance in this *Virola*-resin that, injected into the blood stream, could have properties making it valuable as an arrow-poison. It could also be possible that the hallucinogenic properties of the indoles of the *Virola*-resin act in the manner of an incapacitating substance. It may be of some significance that the Waiká refer to this as a slow-acting arrow-poison and that the hunter must follow the animal, after shooting it, through the forest and wait until the poison has had its effect.

IV.

MYRISTICACEAE

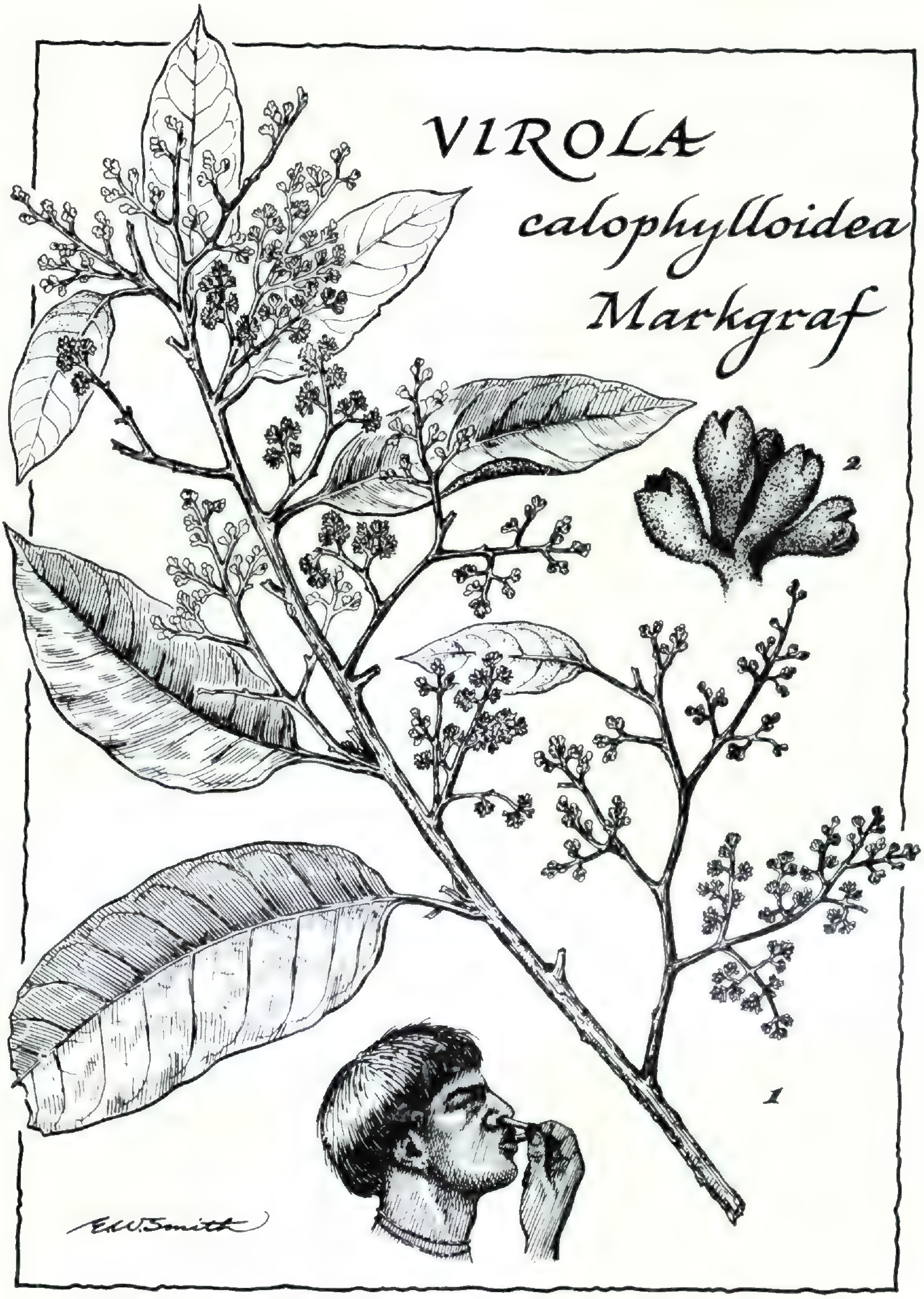
Virola, a rather natural genus of trees or rarely shrubs, comprises under forty-five species distributed in the American tropics, mainly in the Amazon Valley and adjacent humid tropical regions. It is relatively well understood primarily through the monographic works of Warburg and of A. C. Smith, both of which are cited below.

Virola calophylla *Warburg* in Nova Acta Leop. — Carol. 68 (1897) 231; Smith in Brittonia 2 (1937) 474.

Distributed in the Amazonia regions of Colombia, Peru and Venezuela and the western half of the Brazilian Amazon.

One of the most beautiful species of *Virola* with unusually large leaves with well spaced lateral veins.

VIROLA
calophylla
Warburg
2
1
E.W. Smith


VIROLA
calophylloidea
Markgraf
2
1
E.W. Smith

Type of *Virola calophylla (Spruce 3207)* collected along the Casiquiare in Amazonian Venezuela.

COLLECTIONS BASIC TO THIS WORK:

COLOMBIA: COMISARÍA DEL AMAZONAS, Río Apaporis, Soratama. "Small tree about 35 feet tall; diameter 8-9 inches. Bark exudes inside a reddish resin when ripped off tree. Externally reddish brown, pebbled. Puinave=*yá-kee*. Source of narcotic snuff. In flood-forest. June 26, 1951. *R. E. Schultes & I. Cabrera 12855.* — Same locality. "Large columnar tree. Source of *yá-kee*-snuff. Flood forest. August 16, 1951, *Schultes & Cabrera 13587.*

Virola calophylloidea *Markgraf* in Repert. Sp. Nov. 19 (1923) 24; Smith in Brittonia 2 (1937) 475.

Distributed in the Amazonian basin of Colombia and the Amazonas of Brazil.

Type of *Virola calophylloidea (Ule 8846)* collected near Manáos in Amazonian Brazil.

Smith reported this species as rare in 1937, but since that time it has been shown to be relatively abundant, especially in the Colombian Vaupés and Amazonas. It can be distinguished from *Virola calophylla* by its shorter and more compact inflorescences and usually smaller leaves, amongst other characters.

COLLECTIONS BASIC TO THIS WORK:

COLOMBIA: COMISARÉA DEL AMAZONAS, Río Apaporis, Soratama. "Small tree along flood-bank. Flowers brownish. Puinave name= *yá-kee*. Source of narcotic snuff. July 3, 1951. *R. E. Schultes & I. Cabrera 12872.*

Virola theiodora *(Spruce ex Bentham) Warburg* in Nova Acta Acad. Leop. — Carol. 68 (1897) 187; Smith in Brittonia 2 (1937) 470.

Myristica theiodora Spruce ex Bentham in Jour. Bot. & Kew Misc. 5 (1853) 6.

Distributed mainly in the western Amazonia of Brazil and Colombia and probably adjacent Venezuelan territory. Especially abundant in the Rio Negro drainage-area.

Type of *Myristica theiodora (Spruce 1444)* collected near Manáos in Amazonian Brazil.

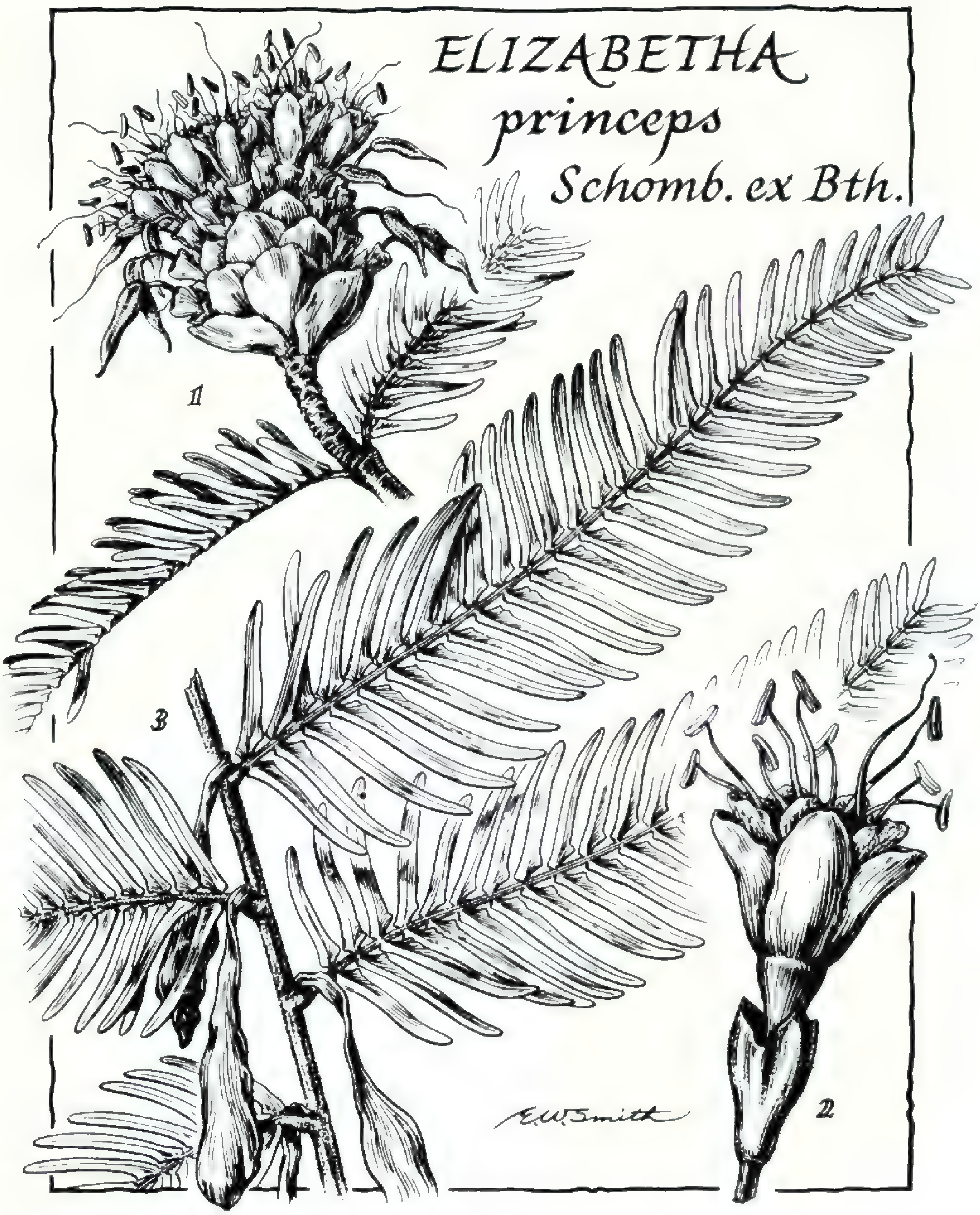
VIROLA
theiodora
(Spr. ex Bth.)
Warburg
2
1
3
E.W. Smith

In Smith's monograph of 1937, *Virola theiodora* is placed in synonymy under *V. elongata* (Spr. ex Benth.) Warb. There can be no misgiving about its relationship to this species but I have preferred to maintain it as distinct because of the ease by which it can be distinguished in the field. When Bentham published *Myristica theiodora*, based on a fruiting specimen, and stated that it seemed to be close to *M. sebifera*, he wrote: "I should nevertheless in the absence of flowers, have considered it a mere variety of that species [*M. sebifera*], had not Mr. Spruce assured me that it is perfectly distinct. The leaves, when drying, are said to emit a strong odour of tea". The crown of *Virola theiodora* appears to be conspicuously denser and more compact than that of what I take to represent *V. elongata*, which has a more freely branching looser crown. The bark of the former seems usually to be thinner and less corky than that of the latter. *Virola theiodora*, furthermore, has, as Smith pointed out, thicker leaves and more prominent lateral veins, and the leaf bases are rounded or subcordate. In addition, the leaf blades in life are lightly but conspicuously sinuous near the margins, a character which my field observations indicate may be more or less peculiar to this species-concept. It is a character recognized by the Waiká Indians who more than once have pointed it out to me whilst we were searching the forests for a *Virola*-tree from which they could extract the resin for preparing snuff.

COLLECTIONS BASIC TO THIS WORK:

BRAZIL: ESTADO DO AMAZONAS, Rio Cauaburí, Maturacá. "Tree 60 feet tall; diameter small. Bark resin red. Bark ingredient of narcotic *epéna*-snuff. Waika=*epéna*. Alkaloid very positive. July 5-August 12, 1967 (R. V. Alpha Helix Expedition Amazon-1967). *R. E. Schultes 24574*. — Same locality and date. "Small tree. Bark resin red. Ingredient of Waika epéna-snuff. *Schultes 24575*.

TERRITORIO DO RORAIMA, Rio Tototobí, Waika Indian village of Wayhana-oo-thle. "Medium sized tree, 60 ft. tall. Bark resin very abundant, reddish brown. Waika=*nya-kwana*. Used for preparing snuff and for smearing on arrows". Alkaloid positive. August 6, 1967 (R. V. Alpha Helix Expedition Amazonas-1967). *R. E. Schultes 24626*.


ELIZABETHA
princeps
Schomb. ex Bth.
1
2
3
E.W. Smith

LEGUMINOSAE

Elizabetha, a genus of some ten species, some of extraordinary beauty, is known only from the northern Amazon and the forests of the Guianas. It is one of the least known South American genera of this family, partly because of the rarity of specimens in herbaria.

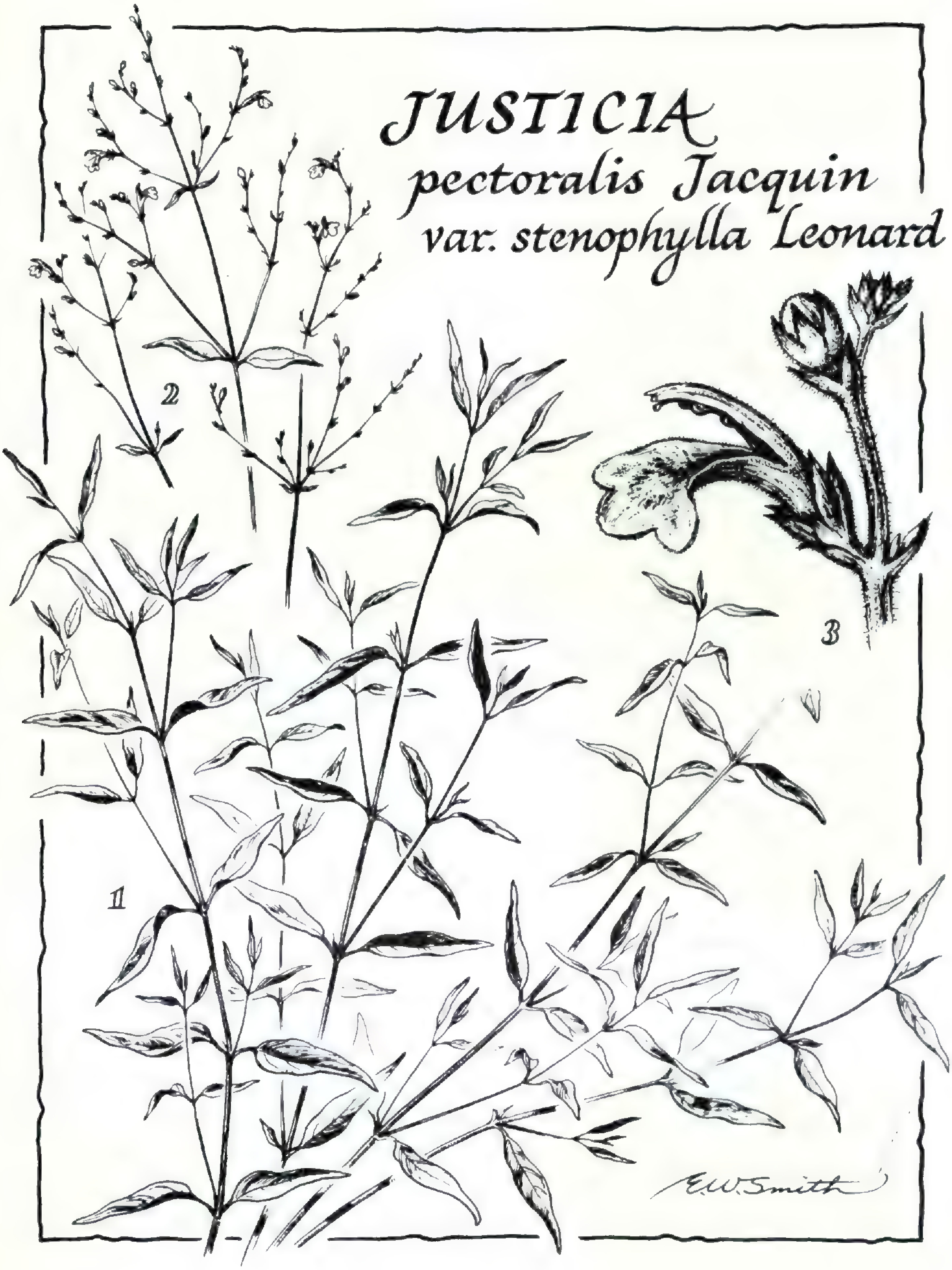
Elizabetha princeps *Schomburgk ex Bentham* in Hooker Journ. Bot. 2 (1840) 92; Ducke in Trop. Woods No. 37 1934) 26; Ducke (1939); Ducke in Bol. Técn. Instit. Agron. Norte 18 (1949) 93.

Distributed in upland forests of the upper and middle parts of the Rio Negro and in the Territory of Roraima in Brazil and in the southern part of British and Dutch Guiana. A beautiful tree of up to ninety feet in height, this species has a very hard and durable wood. The drawing published in this paper is apparently the first time that the species has been illustrated, notwithstanding the fact that it is the type-species of the genus. In fact, no illustrations of any species of *Elizabetha* (with the exception of a flower of *E. Duckei* Huber published in a morphological paper), in spite of the great beauty of these trees and the fact that the genus has been known now for more than a century and a quarter. Type of *Elizabetha princeps* collected by Schomburgk on the upper Parima River near the boundaries of British Guiana, Brazil and Venezuela.

The collections cited below are, unfortunately, sterile. The drawing published in this paper is a composite — leaves of *Schultes 24578* and flowers and inflorescence of *Ducke 328*.

COLLECTIONS BASIC TO THIS WORK:

BRAZIL: ESTADO DO AMAZONAS, Rio Marauiá. "*Ama-azita.*" April 1965. *Georg Seitz 1i.* Estado do Amazonas, Rio Cauaburí, Maturacá. "Bark burnt for ashes to mix with epéna snuff. Tree 40 feet. Bark, petioles alkaloid-negative. Waika=a-ma. July 5-August 12, 1967 (R. V. Alpha Helix Expedition Amazon-1967). *R. E. Schultes 24578.*


JUSTICIA
pectoralis Jacquin
var. stenophylla Leonard
2
3
1
E.W. Smith

ACANTHACEAE

Justicia, a pantropical genus of some three hundred species of herbs or slightly woody plants, has a number of trivial uses in folk-medicine. The leaves of one Asiatic species — *Justicia Adhatoda* — are recognized as having antispasmodic and expectorant properties. *Justicia pectoralis* of tropical America, known in the West Indies as "Jamaica garden balsam" since it is pleasantly fragrant when dried, is employed in South America in the preparation of a pectoral tea, the origin obviously of its specific epithet.

Justicia pectoralis *Jacquin* var. **stenophylla** *Leonard* in Contrib. U.S. Nat. Herb. 31 (1958) 615.

This variety, which grows together with *Justicia pectoralis* is distinguished primarily by its very narrow leaves and may be merely a form of heavy nitrogenous soil near habitations where growth is unusually fast due to an excess of refuse. It is known from the Rio Negro basin of Brazil and from the Colombian Vaupés. In the Rio Negro basin the Indians assert that the herb never flowers.

There are preliminary indications that *Justicia pectoralis* var. *stenophylla* may possess alkaloidal principles.

COLLECTIONS BASIC TO THIS WORK:

BRAZIL: ESTADO DO AMAZONAS, Rio Cauaburí, Maturacá. "Herb. Weed. Used as ingredient of narcotic epena snuff. Alkaloid negative. Waika=*mashihiri*". July 5-August 12, 1967 (R. V. Alpha Helix Expedition Amazon-1967). *R. E. Schultes 24573.*

Territorio do Roraima, Rio Tototobí, Waika Indian village of Wayhana-oo-thle. "Occasionally added dried and pulverized to Waika snuff". August 6, 1967 (R. V. Alpha Helix Expedition Amazon-1967). *R. E. Schultes 24627.*

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JOURNAL OF THE

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NAJAS MINOR ALL. IN NORTH AMERICA[1]

JOUKO MERILÄINEN

Najas minor and *N. gracillima* are somewhat similar in appearance, and their distributions in part overlap. Misidentification by collectors of the rarer species, *N. minor*, is therefore possible. Closer investigation shows, however, that the species are easily distinguishable at any time. Confusingly similar are the narrow leaves and truncate to auriculate sheathing leaf bases. In the latter respect, *N. minor* and *N. gracillima* differ from all the other naiads occurring in North America (except *N. graminea* Del., a tropical introduction to some Californian rice fields).

Seed coat characteristics are conspicuous and visible through the transparent fruit wall, as seen in figures 9 and 10. The areolae can be seen best in dried material, while most other vegetative characteristics are best studied in fresh or resoftened material.

The overall plant size varies greatly in both species. The tallest individuals of *N. minor* are probably those collected by Lauterborn from the Rhine River, Germany, which he

[1]Supported, in part by the Research Committee of the University of Wisconsin on funds (to H. H. Iltis) from the Wisconsin Alumni Research Foundation, by the J. J. Davis Memorial Fund administered by the University of Wisconsin Botany Department, and by Grant 133-2675 of the Wisconsin Conservation Department.

[Research done in 1963-64: In editing this study, the three papers on *Najas minor* All. that have come out since then (Fore and Mohlenbrock 1966; Stookey, Fore, and Mohlenbrock 1964; and Winterringer 1966) were added to make this study more useful. H. H. I.]

TABLE 1

Helpful characteristics in identification of *Najas minor* and *gracillima*

	minor	*gracillima*
COLOR (fresh)	**Dark** green.[2]	**Light** green.[3]
LEAVES	Recurved. Terminal internodes becoming shorter, the leaves tufted at top of branch giving a bushy habit (Fig. 1).	Not recurved.[4] Internodes about equal in different parts of plant, no bushy habit (Fig. 2).
	Leaf margin **curvy.** Base of spinules **many**-celled (Fig. 22-25).	Leaf margin rather **straight.** Base of spinules **few**-celled (Fig. 26, 27).
	Leaves broader, the spinules usually apparent without hand lens.	Leaves very narrow, the spinules usually not visible with the naked eye.
SHEATHING BASE	Truncate to auriculate.	Truncate (rarely to auriculate.
	Rounded. Spinules continuing some distance down shoulders of sheath (Figs. 18, 19).	**Less** rounded. Spinules generally above shoulders only (Fig. 20, 21).
FRUIT	Style relatively **long** (Fig. 4, 7, 8).	Style relatively **short** (Fig. 4, 10, 12).
SEED	Areolae of seed coat **transversely elongate** (Fig. 5, 8, see uppermost cell layer of seed coat in Fig. 14, 15, 16).	Areolae of seed coat **longitudinally elongate,** sunken (Fig. 10, 17).

---

[2]Exception: Baumann (1911, p. 161) ". . . Polster von dunkelbrauner Farbe" in the Lake of Constance (Bodensee) in Central Europe.

[3]Exceptions: a) Fernald & Long 12521, William Co., W. Va., dark green (GH). See Fernald 1947, p. 106 and Clausen 1947, pp. 335-336. b) Seymour 4450a, Bristol Co., Mass., dark green (NEBC).

[4]Difference visible only in fresh or carefully pressed material.

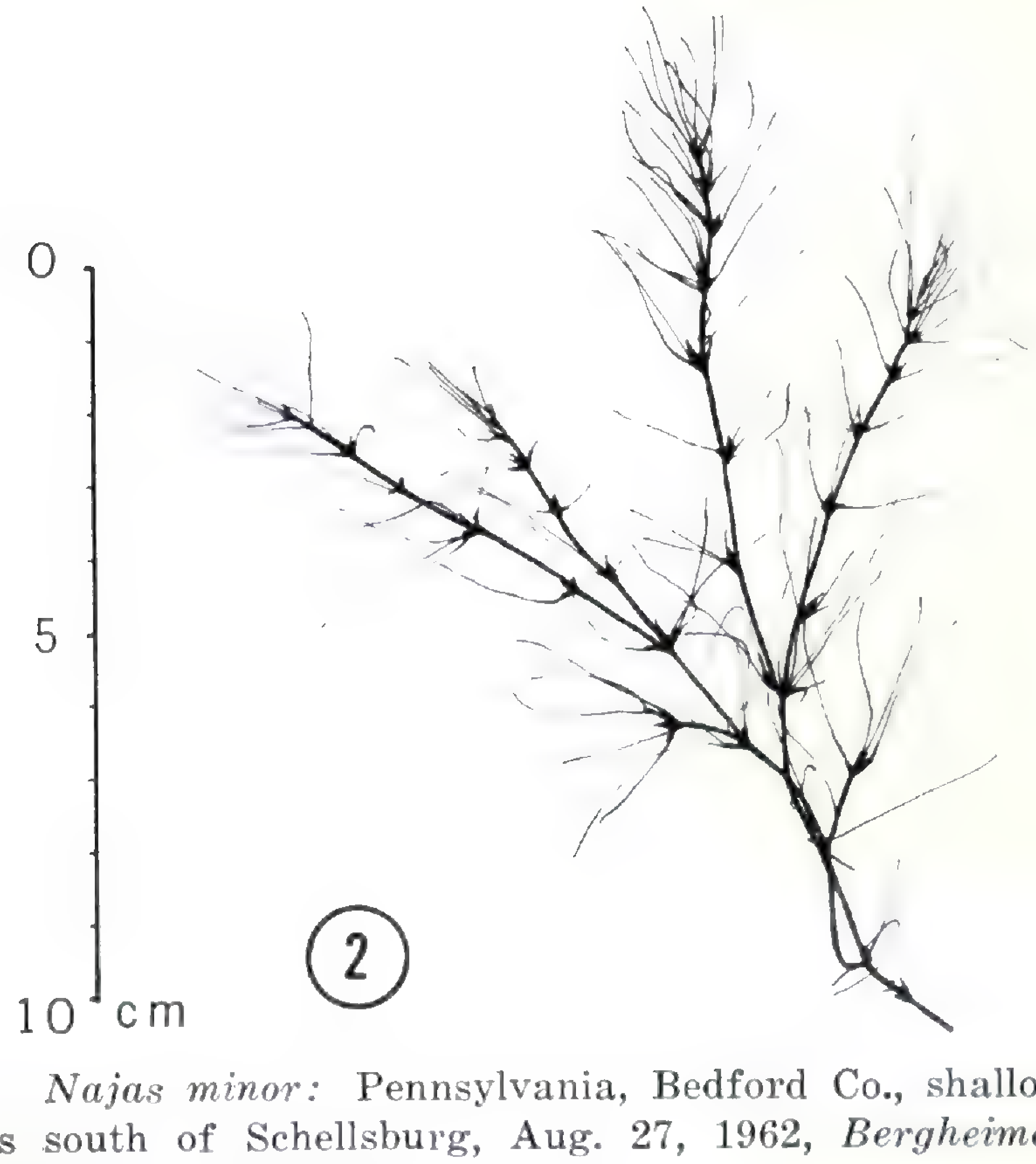


Fig. 1. *Najas minor:* Pennsylvania, Bedford Co., shallow water, 3/4 miles south of Schellsburg, Aug. 27, 1962, *Bergheimer 21371.* (Drawing from photograph).

Fig. 2. *Najas gracillima:* Massachusetts, Norfolk Co., Avon Reservoir, Sept. 22, 1937, *Seymour 5023.* (Drawing from photograph).

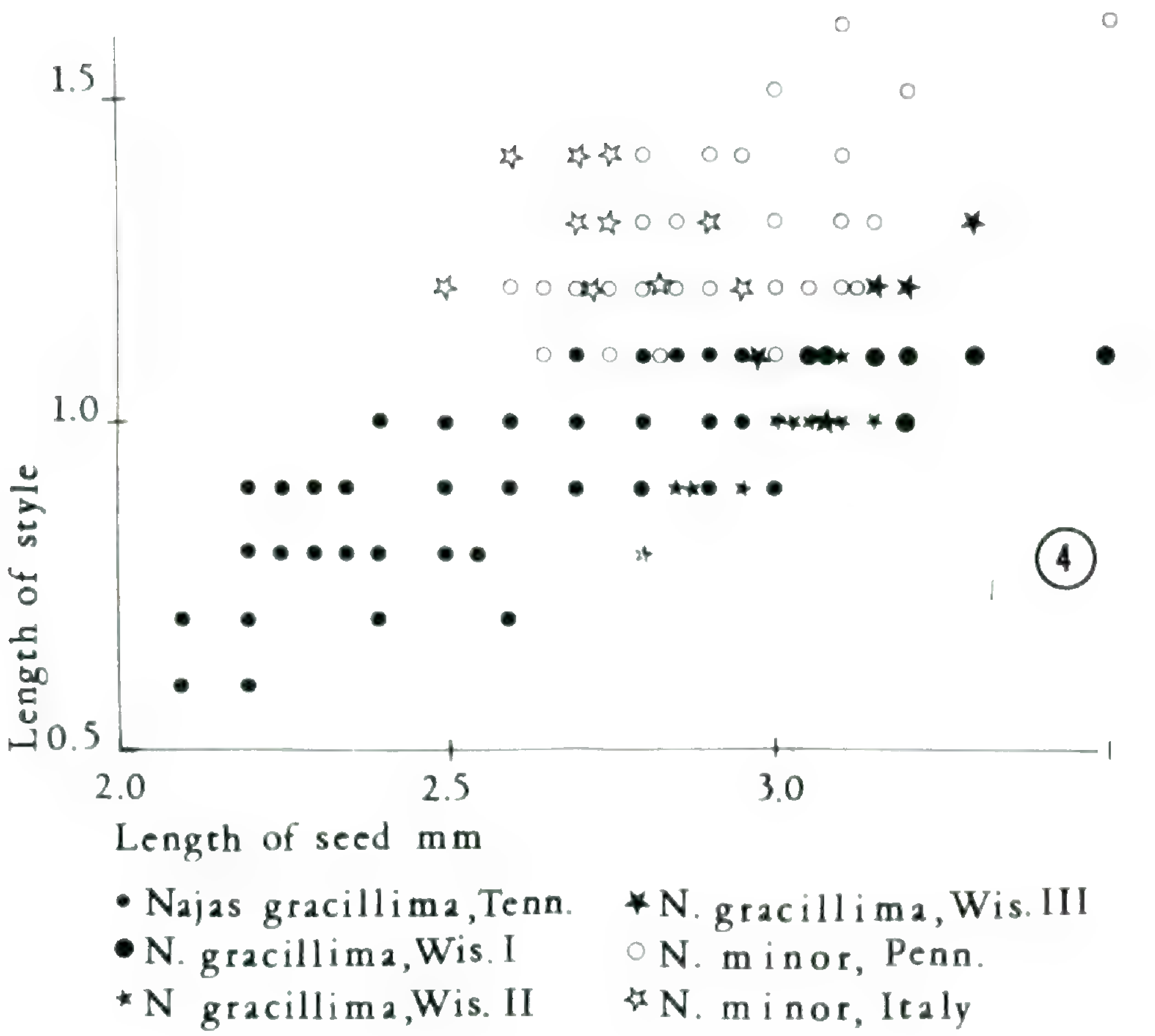
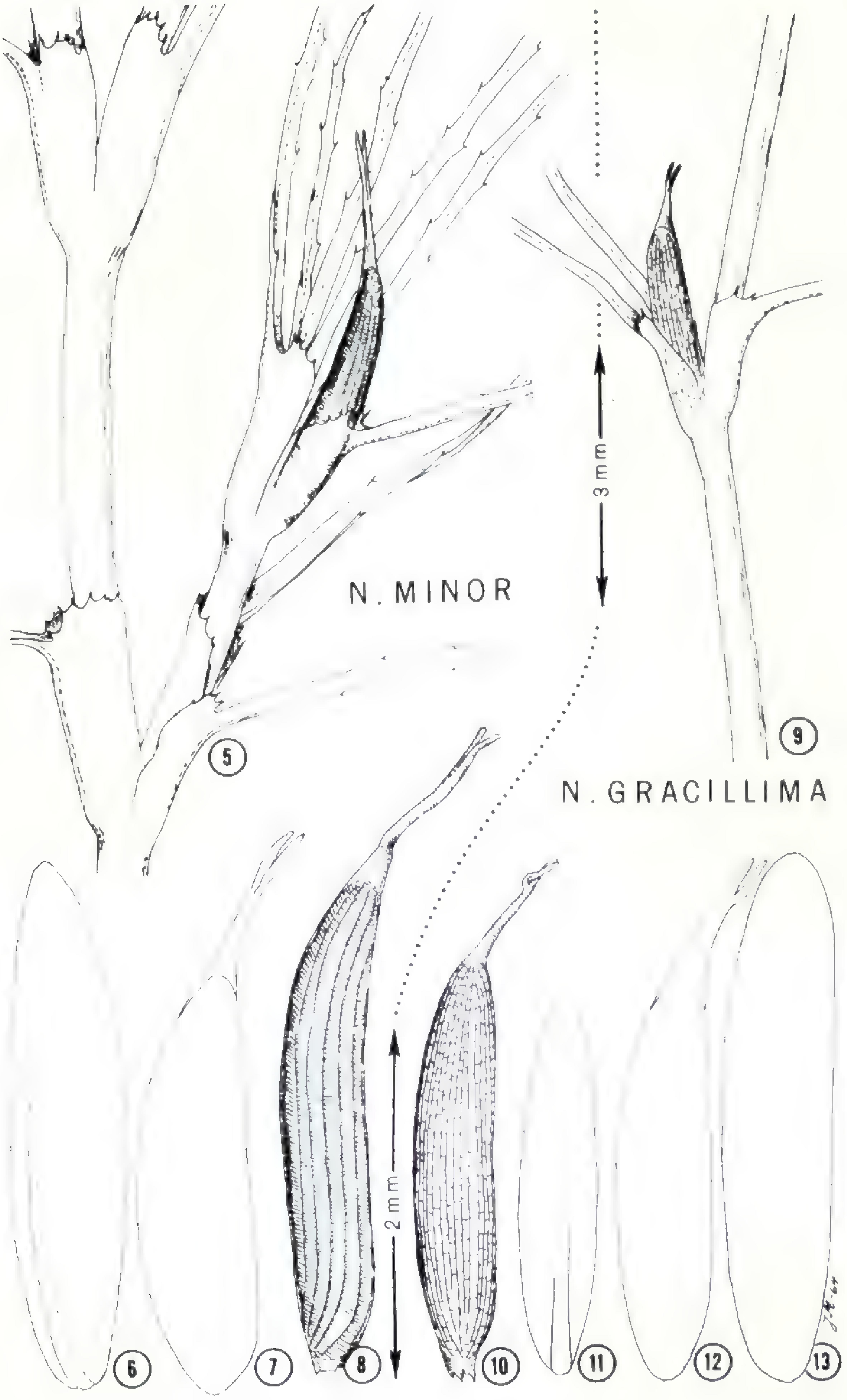


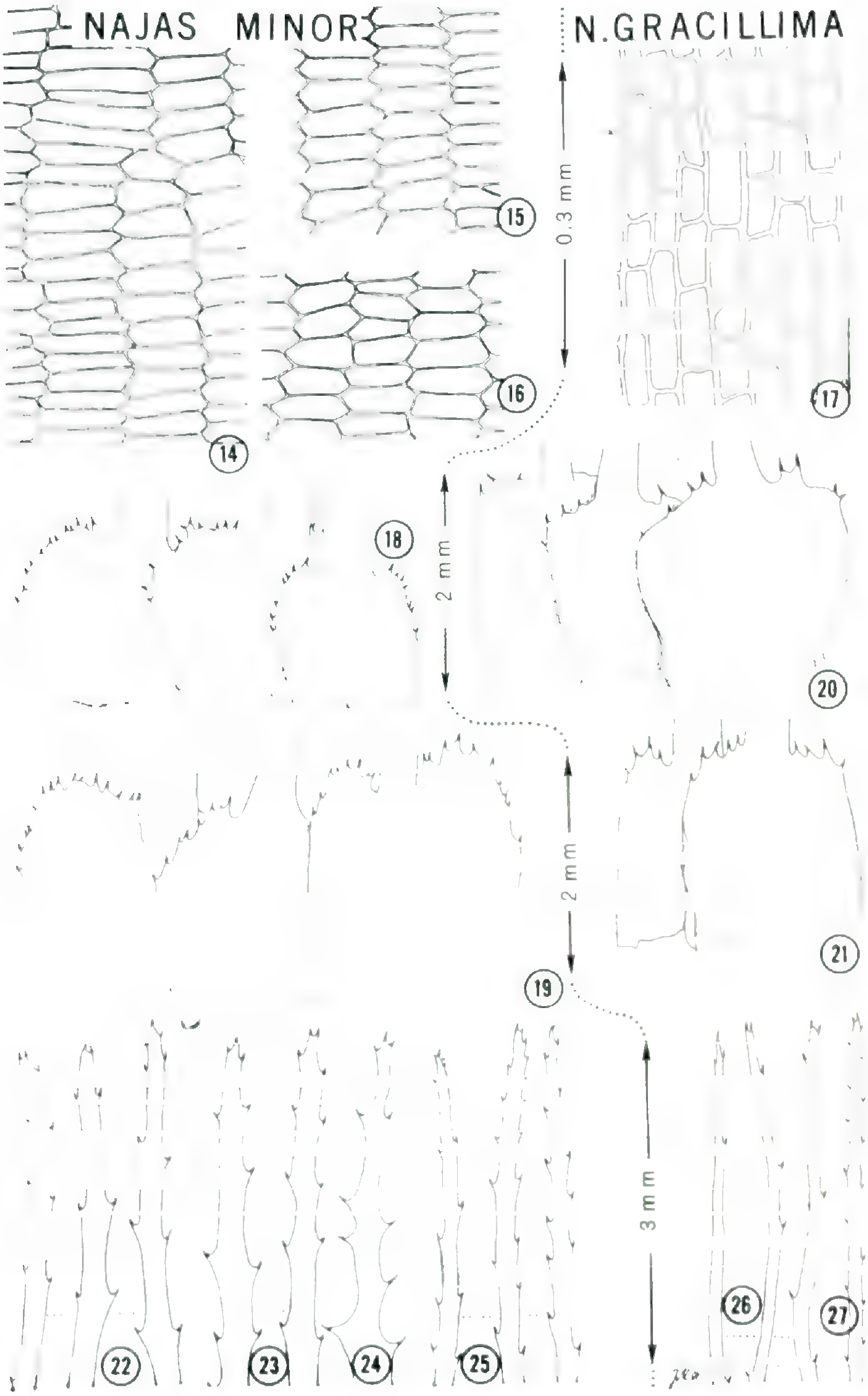
Fig. 4 The style to seed ratio of *Najas minor* and *Najas gracillima*.

reported as 120 cm high (Baumann 1911, p. 160). The number of spinules in leaves also varies and has little if any value in distinguishing these two species.

Najas minor was discovered in America by Muenscher and Clausen in the Hudson River in 1934, and Clausen (1936, p. 338) considered the species an introduction from the Old World. No other localities were found by Muenscher and Clausen although *Najas* material of many eastern North American herbaria was studied (Clausen, 1936, p. 338). In the subsequent thirty years the known North American range of the species has expanded considerably, covering the eastern United States from Lake Ontario west to Illinois and south to northern Florida (cf. Fig. 3,



Figs. 5-13. *Najas minor:* Fig. 5 fruiting branch, Fig. 6 seed, Fig. 7, 8, fruit. *Najas* gracillima: Fig. 9 fruiting branch, Fig. 10, 12 fruit, Fig. 11, 13 seed.



Figs. 14-27. *Najas minor:* Fig. 14, 15, 16 uppermost cell layer of seed coat, Fig. 18, 19 sheathing base of leaf, Fig. 22, 23, 24, 25 tip of leaf.

Najas gracillima: Fig. 17 uppermost cell layer of seed coat, Fig. 20, 21 sheathing base of leaf, Fig. 26, 27 tip of leaf.

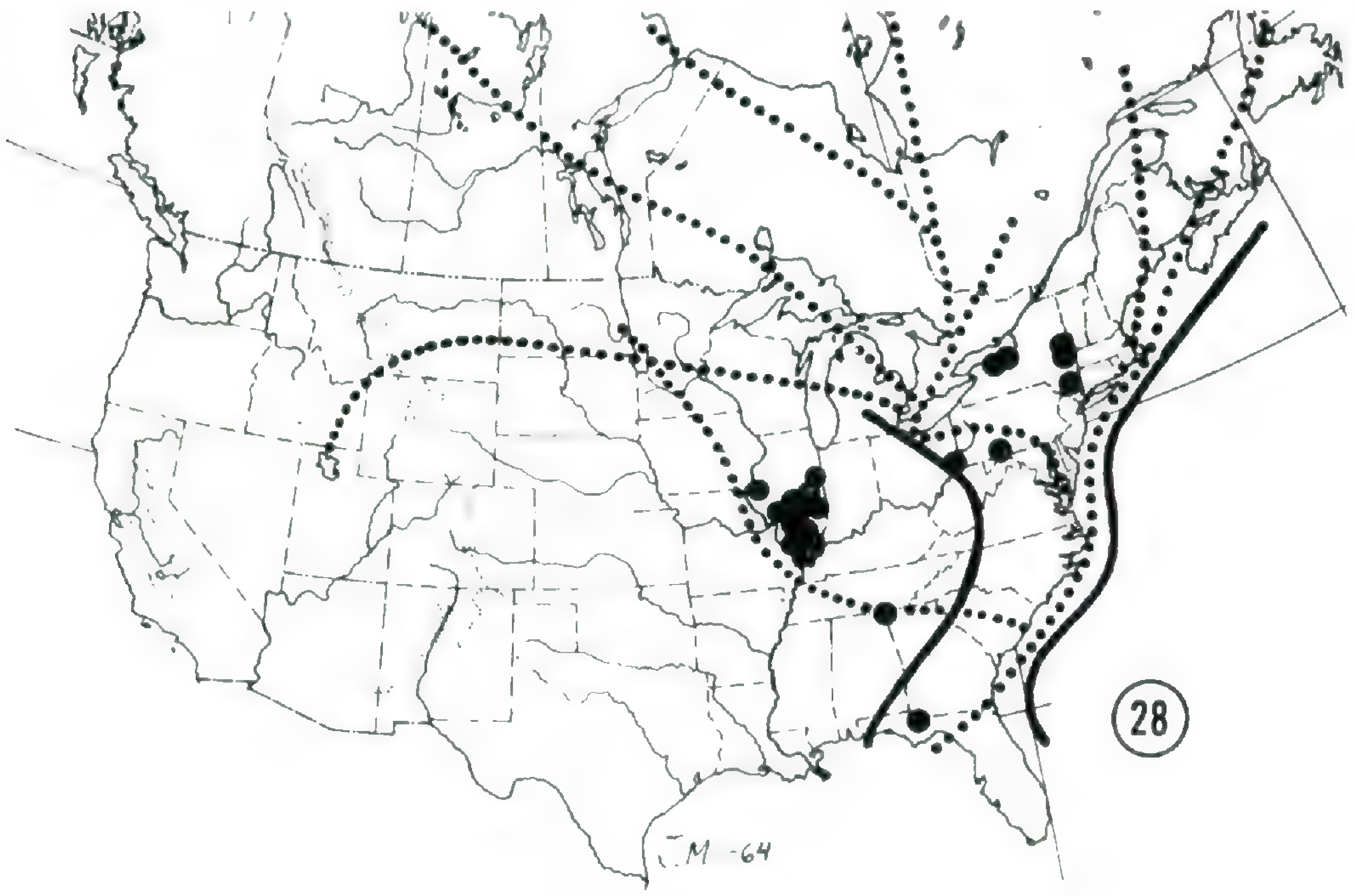
also Stookey, Fore, and Mohlenbrock 1964; Fore and Mohlenbrock 1966). How has this happened? The most important aid in dispersal might have been waterfowl. This factor has been discussed by Chase (1947, pp. 93-97). Shipping might also have been of importance in certain areas, e.g. in New York State as suggested by Chase (1947, p. 94), who reported *N. minor* from the New York State Barge Canal. It would be interesting to know the fate of the *N. minor* material thrown into Cayuga Lake off the Canoga Marshes" (Clausen 1936, p. 338) by W. C. Muenscher in 1935. Some later collections came from the same county, not far from the lake in question!

Most naiads, including *N. minor*, are highly fertile and produce great quantities of fruits, which make them an important food source for ducks, especially since the vegetative parts are eaten too. In the extensive material studied by Martin and Uhler (1939, pp. 9-12) *Najas* as a food source for ducks ranks eighth in importance in the United States and Canada, tenth in "the Atlantic region," and fifth *(N. flexilis)* in "the eastern region". It is likely that submerged plants are relatively more important to diving ducks, and that helophytes, lemnaeids, and nymphaeids are more important to the non-diving ducks. According to Martin and Uhler (1939, pp. 8, 12) 29% of inland divers in North America predominantly feed on plants (excluding the Greater Scaup Duck, see Cottam 1939, p. 33) and in "the eastern region" 52% of the divers eat primarily plants. *Najas minor*, however, growing in many localities on mud flats in shallow water (Baumann 1911, p. 161; Clausen 1936, pp. 337), is available also to non-diving ducks, and even to shore birds.

According to Lincoln (1935) there are four important flyways of waterfowl in North America: the Atlantic, the Mississippi, the Central, and the Pacific. As seen in Fig. 28 the localities of *N. minor* match very well with the Atlantic and Mississippi flyways on the map.

Chase (1947, p. 97) finds "extremely suggestive" the fact that the collected localities of *N. marina* in the Midwest,

The Atlantic Flyway of Waterfowl
with tributary migration routes (after LINCOLN)
And Localities of Najas minor



New York, and Florida are along the Atlantic flyway of waterfowl. This is also an interesting consideration with respect to dispersal of *N. minor.* The distributions of these two species in Europe are similar in freshwater, even if *N. minor* is rarer in the north and more common in the south (Graebner, cited in Backman 1951, p. 9). Furthermore, *N. minor* is "öfters mit *N. marina* (sensu lato) vergesellschaftet" (Glück, cited in Backman 1951, p. 10. See also Kolesnikova 1965, p. 188). In addition, *N. marina* is one of the plants occurring most frequently with *N. minor* in Pliocene and interglacial deposits (Backman 1951, p. 15; Tralau 1959, pp. 401-402).

Furthermore, the first findings of *Najas minor* in America are from the area of several *N. marina* localities. Clausen (1939, p. 179) reports frequent *N. marina* collections from Mendon Pond (Lake Ontario Watershed); Chase mentions *N. minor* from Mendon Pond, Big Mendon Pond, and 100

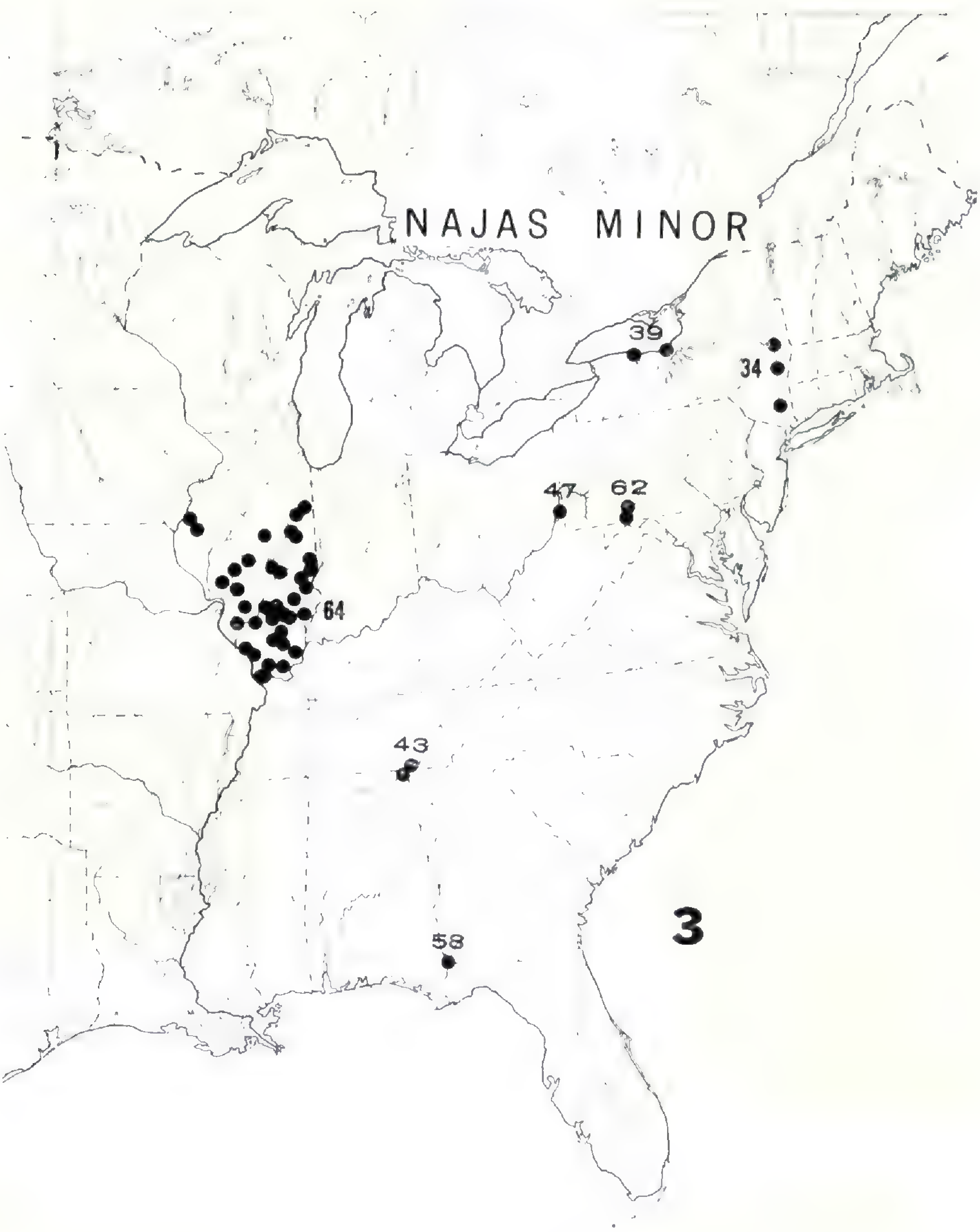


Fig. 3 Distribution of *Najas minor* in North America. Year of first collection indicated.

Acre Pond, all near Mendon, Monroe Co. (Chase, 1947, Table G: Collections deposited in the Cornell University Herbarium). Besides the Atlantic flyway, the Mississippi flyway may also have a significance in the further dispersal of this species. [This is supported by recent reports (Fore and

Mohlenbrock 1966; Stookey, Fore, and Mohlenbrock 1964; Winterringer 1966) of its great frequency (Fig. 3) in the southern half of Illinois. It is interesting that in a state as well-collected for aquatics as Wisconsin, of the three known stations of *N. marina*, two were collected in the past three years and all from near the shore of Lake Michigan, a well-known flyway for birds. (Sheboygan Co.: Random Lake, 1941, *Posekany s.n.* (WIS). Racine Co.: Long Lake, 1965, *Lind 88* (WIS). Kenosha Co.: Wind Lake, 1963, *Meriläinen 637* & *638* (WIS)). H.H.I.]

Many European localities of *N. minor* are associated with great, slow rivers, or oxbow lakes of the Rhine in Germany, the Danube in Austria, the Oder in Poland, and the Volga in the Soviet Union. This suggests a considerable tolerance to pollution. In most cases *N. minor* localities are also in large rivers in America (the Hudson, the Ohio, and the Tennessee Rivers) and the species is, according to Chase (1947, p. 95) much more tolerant of polluted conditions than *N. flexilis*.

We have already referred to some plants occurring with *N. minor*. Some more data will yet be given, even though there are risks in comparing floras of localities studied by different investigators using different methods for different purposes. Certainly also the size of localities is very variable. We do not always know the identity of the ecological requirements of plants reported under the same name from Europe and America. It is hoped, however, that the co-occurring flora of *N. minor* gives some indication of the ecology of this species.

Tralau (1959, pp. 398-402) makes a most interesting comparison between the interglacial flora of Lichvin in the Kaluga district, Russia, reported by Sukatchev, and a recent local flora in the westernmost Ukraine, 1000 km to the south-west, studied by Kleopow. In both districts *N. minor* was reported. Not only the acquatic but the forest flora as well are identical. The aquatic species co-occurring with *N. minor* are *Najas marina*, *Potamogeton crispus*, *P. acutifolius*, *P. natans*, *Stratiotes aloides*, *Scirpus lacustris*, *Eury-*

ale ferox, *Ceratophyllum demersum* and *Trapa natans*. Only one species, *Euryale*, is absent from the modern Ukrainean flora, and Tralau (1959, p. 402) suggests that this extinction was caused by historical factors. He further states that the former climate in the Lichvin district "may have been more oceanic than it is now." In data collected by Backman (1951, p. 15) from 16 Pliocene and interglacial deposits, *N. minor* occurs with *Ceratophyllum demersum* in 14, *Alisma plantago* in 12, and with *Potamogeton trichoides*, *Najas marina*, and *Trapa natans* in 10 localities. *Najas minor* has been found from only very few post-glacial deposits, two of which are in Finland. *Trapa natans* occurs in both of these, and *Najas marina*, *N. flexilis*, and *N. tenuissima* have been located in one of them (Backman 1951, pp. 17-23).

In comparing three recent river localities of *N. minor*, two north of the Black Sea and one in Rostock, Germany,[5] we find *Potamogeton crispus*, *Hydrocharis morsus-ranae*, *Sagittaria* s.(p.) and *Ceratophyllum demersum* in all of them, and *Potamogeton pectinatus* in Rostock and one of the Soviet Union localities. Found in both Soviet Union localities are *Typha latifolia*, *Spirodela polyrhiza*, *Lemna minor*, *Butomus umbellatus*, *Alisma plantago-aquatica*, *Cicuta virosa* and *Oenanthe aquatica*. In one of the localities occur *Najas marina* and *Trapa natans* (Backman, 1951, pp. 10-11).

From America, Clausen (1939, pp. 170, 175) reports *N. minor* from Braddock Bay and Sterling Pond, both of which connect with Lake Ontario. The associated flora in both places includes *Typha latifolia*, *T. angustifolia*, *Potamogeton pusillus*, *Elodea canadensis*, *Vallisneria americana*, *Spirodela polyrhiza*, *Lemna trisulca*, *L. minor*, *Wolffia punctata*, *Heteranthera dubia*, *Ceratophyllum demersum*, and *Myriophyllum exalbescens*.

There is little information concerning the ecology of *N. minor*, but it may be partly summarized as follows: the species thrives in eutrophic waters, growing on mud bot-

[5]Only place in Europe where *N. minor* occurs in slightly brackish water (Backman, 1951, p. 10).

toms at a depth of one to more than ten feet of water. Often associated with large rivers or blind river-beds (oxbow lakes) it profits by river "improvement" projects in America, and tolerates pollution in some degree. The fruits resist considerable drought.

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The writer wishes to express his sincere appreciation to Professor Hugh H. Iltis, Curator of the University of Wisconsin Herbarium, for all his advice and encouragement, for the inspiring working environment and especially for the valuable additions to up-date the paper during the years of editing. Without his help this paper could not have been written.

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LOCALITIES OF NAJAS MINOR[6]
(See Clausen, 1936, 1939 and Chase 1947)

NEW YORK: A. Drainage basin of Hudson River: ALBANY Co. Watervliet Reservoir, Sept. 3, 1934, *Muenscher & Clausen 4282* (CU). COLUMBIA Co. About one mile south of Stuyvesant, Aug. 28, 1934, *Muenscher & Clausen 4280* (CU). In channel west of Rogers Island, Hudson River, Sept. 1, 1936, *McVaugh 4460* (GH). Kinderhook Lake, Aug. 26, 1942, *Chase NY-50* (CU). Kinderhook Lake, Sept. 18, 1946, *Chase NY-205* (CU). DUTCHESS Co. Mouth of Wappinger Creek, Hudson River, New Hamburg, Aug. 31, 1936, *Muenscher & Curtis 5502 & 5503* (GH, WIS). Mouth of Wappinger Creek, Hudson River, Aug. 28,

[6]Many specimens have been seen in other herbaria than mentioned in this paper before the species became of special interest to the writer. The specimens in CU, the Cornell University Herbarium, and those recently collected from Illinois were not examined by the author.

1942, *Chase NY-57* (CU). RENSSELAER CO.: Junction of Mohawk and Hudson Rivers, Troy, Sept. 10, 1935, *Muenscher & Curtis 4826* (GH). SARATOGA CO: Mouth of Mohawk River at Waterford, Aug. 21, 1934, *Muenscher & Clausen 4279* (CU). Mouth of Mohawk River at Waterford, Aug. 22, 1934, *Muenscher & Clausen 4281* (GH). Backwater of Mohawk River, Waterford, Sept. 10, 1935, *Muenscher & Curtis 4825* (GH). Hudson River, Mechanicsville, Aug. 7, 1938, *Muenscher & Justice s.n.* (GH, WIS). Hudson River above Mechanicsville, Aug. 27, 1942, *Chase NY-44* (CU). Junction of Mohawk and Hudson Rivers, Aug. 27, 1942, *Chase NY-45* (CU). Waterford, Sept. 17, 1946, *Chase NY-202* (CU). B. Lake Ontario watershed: CAYUGA CO: Sterling Pond, connected with Lake Ontario by a narrow channel, North Fair Haven, Sterling Township, Aug. 10, 1939, *Clausen & Hinkey 4326* (GH, NY). Menard Memorial Bridge, Seneca River, Sept. 1, 1942, *Chase NY-65* (CU). MONROE CO: East side of Salmon Creek Inlet to Braddock Bay, Greece Township, Aug. 27, 1939, *Clausen & Hinkey 4264* (GH, NY). 100 Acre Pond, Mendon, July 27, 1946, *Chase NY-176* (CU). SENECA CO: Menard Memorial Bridge, Seneca River, July 10, 1946, *Chase NY-105* (CU). Chase (1947) reports in text the following localities that are not in Table G, which was used in the above list: New York Barge Canal, Big Mendon Pond (p. 38), and Mendon Pond (p. 90). PENNSYLVANIA: BEDFORD CO: Shallow water, ¾ miles south of Schellsburg, Aug. 27, 1962, *Berkheimer 21371* (PENN, WIS). Edge of dam, 3⅜ miles south of Centerville, Sept. 18, 1962, *Berkheimer 21584* (PENN). WEST VIRGINIA: OHIO CO: Ohio River, east side of Wheeling Island, shore along north end of island, Sept. 26, 1947, *Bartholomew s.n.* (GH, WVA: Core, private communication[7]). TENNESSEE: MARION CO: July 17-23, 1944, *Muenscher & Isely s.n.* (WVA: Core, private communication). Hales Bar Reservoir, near dam, July 18, 1944, *Isely s.n.* (US). ALABAMA: JACKSON CO: Goosepond. Guntersville Reservoir, July 2, 1943, *Isely s.n.* (GH, NY). FLORIDA: JACKSON CO: Lake Seminole, north of Sneads, Oct. 28, 1958, *Godfrey 57873* (FSU[8], GH, NY). Lake Seminole, north of Sneads, Aug. 16, 1961, *Godfrey 61393* (FSU, NY).

ILLINOIS: (In view of the very large number of Illinois collections of *Najas minor*, almost all of which are in the Illinois State Museum Herbaria, only the first collection made in each county is listed, H.H.I.) ALEXANDER CO: Horseshoe Lake, Olive Branch, June 22, 1964, *Allen*. CHAMPAIGN CO: R. D. Kibler farm, ½ mile south of Mayview, July 20, 1965, *Fritz*. CLARK CO: Lincoln Trail Lake, 2 miles south of

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[7]Thanks are expressed to Dr. Core for his help during the study.

[8]The special thanks of the writer are due to Dr. Godfrey for the excursion to the lakes of northern Florida and for his kindness during herbarium study. This trip was partly supported by the J. J. Davis Fund, of the Department of Botany, University of Wisconsin.

Marshall, July 27, 1964, *Miller*. CLINTON CO: Trenton Sportsman's Club, 4 miles north of Trenton, Aug. 11, 1964, *Miller*. CRAWFORD CO: Country Club Pond, Robinson, Aug. 11, 1965, *Fisher*. DEWITT CO: Weldon Spring Lake, 3 miles southeast of Clinton, June 23, 1965, *Stinauer*. EDGAR CO: Paris East Lake, Paris, July 27, 1965, *Fritz*. FORD CO: Hopples Pond, 6 miles northwest of Roberts, June 15, 1965, *Hiltobran*. FRANKLIN CO: West Frankfort New Reservoir, 1 mile southwest of Thompsonville, July 9, 1964, *Allen*. GALLITIN CO: Pounds Hollow Lake, 5 miles northeast of Karbers Ridge, Aug. 4, 1964, *Allen*. GREENE CO: Greenfield City Lake, 1 mile east of Greenfield, Aug. 4, 1964, *Lockhart*. HAMILTON CO: McLeansboro Reservoir, 1 mile west of McLeansboro, Sept. 14, 1965, *Allen*. HENDERSON CO: Smith Pond, 5 miles southwest of Raritan, Aug. 3, 1965, *Russell*. IRIQUOIS CO: Storm's Pond, 3 miles northeast of Crescent City, Aug. 26, 1964, *Zebrun*. JACKSON CO: Lake Murphysboro, 1 mile west of Murphysboro, June 24, 1964, *Miller*. JEFFERSON CO: Miller Lake, 7 miles northeast of Mt. Vernon, July 29, 1964, *Fisher*. JOHNSON CO: Ferne Clyff Lake, 1½ miles southwest of Goreville, June 9, 1964, *Allen*. MCDONOUGH CO: Argyle Lake, 2 miles north of Colchester, June 23, 1964, *La Buy*. MACOUPIN CO: Staunton City Lake, 2 miles north of Staunton, June 22, 1964, *Lopinot*. MADISON CO: Henry Haag Pond, 2 miles northeast of Godfrey, Sept. 3, 1964, *Lockhart*. MARION CO: Salem Reservoir, northwest edge of Salem, July 13, 1964, *Fisher*. POPE CO: Lake Glendale, 3 miles south of Glendale, Aug. 4, 1964, *Allen*. PULASKI CO: America Lake, 4 miles east of Mounds, Aug. 5, 1964, *Allen*. RANDOLPH CO: Randolph County Lake, 5 miles northeast of Chester, June 15, 1964, *Miller*. RICHLAND CO: Albert Ax Lake, 9 miles northwest of Olney, Aug. 24, 1965, *Fisher*. ST. CLAIR CO: Al Reibel Lake, 4 miles southeast of Freeburg, June 14, 1965, *Miller*. SALINE CO: John Griffin Pond, 3 miles west of Raleigh, Sept. 14, 1964, *Allen*. SANGAMON CO: Carl Moore Pond, 2 miles west of Rochester, Aug. 31, 1964, *Rogers*. SHELBY CO: Bessie Grover Pond, 5 miles east of Strasburg, July 19, 1965, *Fritz*. WABASH CO: Highland Hills Water, 2½ miles southeast of Lancaster, Aug. 23, 1965, *Fisher*. WASHINGTON CO: Washington County Conservation Area Lake, 5 miles south of Nashville, July 18, 1966, *Dolbeare 886*. WAYNE CO: Artificial Lake, Johnsonville, Oct. 15, 1963, *Lopinot*.

ILLUSTRATIONS

Figs. 1, 2, 8, and 10 were drawn using dry material; for all the other illustrations the plants were resoftened. Fig. 6-27 were drawn with the aid of camera lucida. The following material was used for figs. 5-27. NAJAS MINOR: Pennsylvania, *Berkheimer 21371* (PENN), figs. 5, 8, 16, 19, 25; Torino, Italy, Aug. 22, 1909, *Ferrari* s.n. (WIS), figs. 6, 15, 18, 22; New York, *Muenscher & Curtis 5503* (WIS), figs. 7, 14, 23; Pennsylvania, *Berkheimer 21584* (PENN), fig. 24. NAJAS GRACILLIMA: Tennessee, Chickasaw State Park, Aug. 18, 1954, *Iltis* s.n.

(WIS), figs. 9, 10, 11, 12, 17, 20, 26; Massachusetts, Norfolk Co., Sept. 22, 1937, *Seymour 5023* (WIS), figs. 13, 21; Massachusetts, Franklin Co., Aug. 3, 1925, *Seymour 2472* (WIS), fig. 27.

HERBARIUM, UNIVERSITY OF WISCONSIN, MADISON
AND DEPARTMENT OF BOTANY,
UNIVERSITY OF HELSINKI, FINLAND

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CONTRIBUTIONS TO THE FLORA OF NOVA SCOTIA. IX. HABITAT STUDIES OF ARCTIC-ALPINE AND BOREAL DISJUNCT SPECIES[1]

R. W. HOUNSELL[2] AND E. C. SMITH

The flora of Nova Scotia contains many species of disjunct distribution. In the southwestern section of the province are found species that are usually associated with the Atlantic Coastal Plain of the United States. Roland (1947) discussed this element, listing such species as *Rhexia virginica* L. and *Woodwardia aerolata* (L.) Moore. In recent years exploration in northern Cape Breton by the junior author and his forest ecology field crews from Acadia University has resulted in a growing list of species with northern affinities (e.g., Smith and Schofield, 1952; Smith and Erskine, 1954). That these Arctic-alpine and boreal disjunct species have two centres of distribution in Nova Scotia (viz. the northern Cape Breton area and the Minas Basin-Bay of Fundy area) was shown in a previous paper (Hounsell and Smith, 1966). The aim of the present paper is to describe some of the small, isolated stations harboring these species and hence to shed some light on the twin problems of their disjunction and persistence.

Northern Cape Breton Island comprises a region of highlands surrounded by a narrow coastal plain which accommodates a highway known as the Cabot Trail. This road links the seaside villages but makes few incursions upon the inland and upland wilderness about one half of which is within the Cape Breton Highlands National Park. Although the terrain rises but little above 1500 feet it is dissected by many narrow, steep river gorges where the bog-fed rivers that originate in the flat, central uplands channel their way to the coast. The sheer wet cliffs found at the many water-

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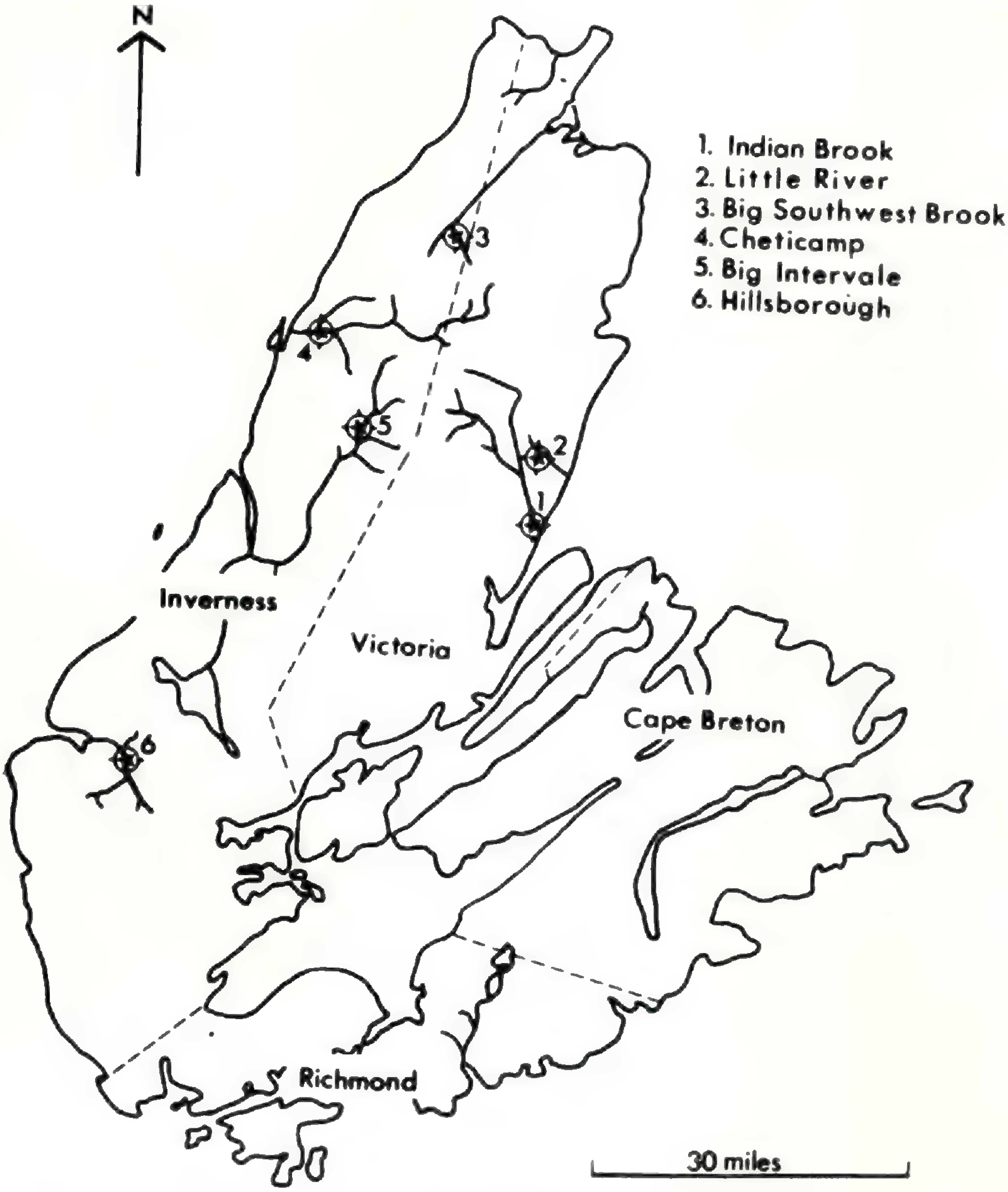
[2]Present address Department of Biology, Queen's University, Kingston, Ontario.



Map of Cape Breton Island, Nova Scotia

falls and at other points along the gorges provide suitable habitats for Arctic-alpine and boreal disjuncts.

Practically every river valley examined to date has been shown to possess one or more disjunct stations, none of which is very extensive in size; some are a few hundred yards long, others much smaller. Some provide an acceptable niche for only one species, but most harbor several. Of the 58 species included in this study the largest number

found at one station is 27, at Big Southwest Brook. Lockhart Brook, flowing into the Salmon River, follows closely with twenty-five. These two stations are by far the richest in species number.

In an attempt to determine those environmental factors that have allowed the relic northern flora to survive in isolated pockets, presumably for 8,000 years or so, a study was made of the habitats at six stations in northern Cape Breton (Fig. 1) in the summer of 1964. Each station consisted of a river-valley cliff-face with its associated talus slope. The talus and that part of the cliff which was accessible were examined both for vegetation and variation in habitat. A species list was made for each small detectable change in habitat and the relative commonness of each species was noted, not only for disjuncts but also for those species of the surrounding forests, river gravels and fields that had been able to invade the cliff habitat. Rock and soil samples were taken at each site for later analysis. Note was made of the extent, sheerness and stability of the cliff and talus, of degree and direction of exposure and of seepage.

(A) INDIAN BROOK, VICTORIA COUNTY

The Indian Brook station is located on the south side of the stream about one half mile west of the Cabot Trail at a river elevation of 50 feet above sea level. Nichols (1918), in the course of his study of the vegetation of northern Cape Breton Island, travelled extensively in this general area and collected a number of disjuncts but made no reference to this small but rich colony; it was not until 1952 that this station was discovered.

Indian Brook runs through a deep gorge whose steep sides rise, in steps, at least 200 feet, often from the very edge of the stream. The cliffs are not continuous but interrupted by steep wooded slopes such as those which flank the disjunct station.

A fan-shaped talus slope extends from the river's edge up to a sheer cliff which rises about 70 feet beyond the talus. A dike on the east side and a deep chimney-like crevice on the west side separate the main part of the cliff

from two adjacent sections. The bases of these side cliffs slope downward from the top of the talus until they reach to within a few feet, vertically, of the summer water level at a horizontal distance of 30 feet from the river. All three sections of the cliff are mainly north-facing but the eastern section has a considerable extent of west-facing surface. The horizontal measurement of the cliff is approximately 220 feet.

Above these cliffs the forest extends up the steep and terraced slope to the relatively flat area above the gorge. On each side the forest descends practically to the water's edge but bands of herbaceous vegetation, growing among boulders that are water-covered in the spring, separate it from the river.

Near its base at the spring water level, the talus measured 56 feet across and consisted mainly of boulders, two to three feet long, that had once been part of the cliff. Between these partially weather-smoothed boulders small pockets of soil have accumulated, possibly through filtering from above, supporting a sparse but varied strip of vegetation. Among the herbaceous plants seen were *Satureja vulgaris* (L.) Fritsch, *Carex intumescens* Rudge, *Thalictrum polygamum* Muhl. and *Taraxacum officinale* Weber. All of these are common constituents of the Nova Scotian flora.

In the finer, less stabilized talus, farther up the slope, occurred such common plants as *Anaphalis margaritacea* (L.) C. B. Clarke var. *intercedens* Hara, *Achillea millefolium* L., *Hieracium pilosella* L. and *Solidago flexicaulis* L. On the talus, as well as on the sheerest of faces, was found *Campanula rotundifolia* L.; this proved to be one of the commonest plants at all the stations visited.

The main, north-facing cliff is sheer but broken by numerous small crevices and cracks. At the time of visiting most of it was extremely dry; only near the base where the rock is much fractured and crumbled was there evidence of seepage. In this section, in rather dry pockets of soil on narrow ledges, two boreal disjuncts, *Arabis hirsuta* (L.)

Scop. var. *pycnocarpa* (M. Hopkins) Rollins and *Draba arabisans* Michx., were noted. *Saxifraga aizoon* Jacq. var. *neogaea* Butters, an Artic-alpine species, was also collected from this cliff section.

A soil sample taken from a deep pocket at the cliff-base had a pH of 6.9. The exchangeable calcium and magnesium were both comparatively low (Table I).

TABLE I

ANALYSES OF SOIL SAMPLES

(Ex. Ca. — exchangeable calcium in M. eq.; Ex. Mg. — exchangeable magnesium in M. eq.)

STATION	pH	EX. Ca.	EX. Mg.	REMARKS
INDIAN BROOK "A"	6.9	1.60	0.34	Crevice at base of sheer cliffs, above talus.
INDIAN BROOK "B"	6.1	1.00	0.22	Moss-mat, sloping cliff, with *Saxifraga aizoon* var. *neogaea*.
INDIAN BROOK "C"	6.3	7.89	2.70	Dry cliff ledge — *Draba arabisans* and *Arabis hirsuta* var. *pycnocarpa*.
LITTLE RIVER	6.5	3.02	1.55	Ledge in damp grotto.
BIG SOUTHWEST "A"	3.8	0.89	1.64	Dry, grassy west-facing ledge with *Carex capillaris* var. *major*.
BIG SOUTHWEST "B"	5.6	5.08	5.20	Wet ledge below main cliff, east-facing, *Scirpus cespitosus* var. *delicatulus*.
CHETICAMP	5.9	2.85	4.65	Wet, north-facing ledges, *Achillea borealis, Scirpus cespitosus* var. *delicatulus*.
BIG INTERVALE	4.6	3.58	6.20	Dry ledge — *Arabis drummondi, Woodsia ilvensis*.
HILLSBOROUGH	7.3	9.08	1.55	Limestone cliff — *Cystopteris bulbifera, Cryptogramma stelleri*.

Fine talus, harboring no disjuncts, covers the floor of the slanting dike that serves as the eastern delimitation of the

main cliff. Immediately to the north of the dike the eastern cliff of the three-parted complex has a small face exposed to the northwest and a more extensive, almost vertical face exposed to the north. The northwest face has a slope of about 45 degrees. Seepage was evident on the bottom half, leaving the upper section dry and practically devoid of plant life. Low moss mats and crustose lichens covered much of the moist section of the unbroken rock surface. *Saxifraga aizoon* var. *neogaea* was the only vascular plant present in the limited anchorage and soil available.

A soil sample taken from the moss-*Saxifraga* mat was later found to have a pH of 6.1. Exchangeable calcium and magnesium were both low. Rock taken from this cliff section was identified as syenite — an acidic rock with feldspar and probably mica.

Grassy ledges of the western cliff supported, in addition to wide-ranging species such as *Campanula rotundifolia* and *Hieracium canadense* Michx., patches of disjuncts, including *Draba arabisans, Arabis hirsuta* var. *pycnocarpa, Woodsia ilvensis* (L.) R. Br., *Poa glaucantha* Gaudin, and *Achillea borealis* Bong. These grew on exposed, dry ledges which received much shade from small trees that had, here and there, gained a foothold. *Cystopteris fragilis* (L). Bernh. var. *laurentiana* Weath., a boreal disjunct, occurred frequently in the lower crevices but the commonest occupant of the basal, seepy areas was *Woodsia ilvensis* which was able to thrive in the tiniest of niches. A soil sample taken from a narrow ledge that supported *Draba arabisans* and *Arabis hirsuta* var. *pycnocarpa* was found to have a pH of 6.3 and correspondingly low values for exchangeable calcium and magnesium. Both of these species have been described as calcicoles by Scoggan (1950) and others but here they are found in the soil with much less calcium and a lower pH than they seem to prefer in Gaspé and Bic.

The lower section of the western cliff is quite different from the more exposed, mainly dry upper half described above. It is about 30 feet high and 85 feet long, set back

40 feet from the summer water level and 15 feet above it. Large deciduous trees growing between it and the river provide continual shade during the summer. The upper 20 feet of the sheer cliff is relatively dry, supporting but a few mosses and lichens but throughout the lower ten feet seepage was extensive, soaking the crevices and ledges and forming small pools in the basal grottoes.

Because of the deep shade and the continual supply of water this habitat was much cooler than those of the surrounding, more exposed and drier cliffs. *Woodsia ilvensis*, *W. glabella* R. Br. and *Asplenium viride* Huds. were common in the very wet grottoes, while *Carex atratiformis* Britt., *Arabis hirsuta* var. *pycnocarpa* and *Achillea borealis* were fairly common ledge - dwellers, all being disjunct species. *Sedum rosea* (L.) Scop., which is found well into the Arctic regions but is also known from many stations in Nova Scotia, was common on the almost vertical walls, growing out of very small cracks. Another common plant was *Erigeron hyssopifolius*, Michx., a boreal and alpine species.

Among the plants which occurred at the lateral edge of the lower half of the talus, where stablization was well advanced, were several which, while not disjuncts, are still of interest as pioneers on talus slopes. *Aralia racemosa* L. and *Rhus radicans* L. var. *rydbergii* (Small) Rehd. (two calciphytes) were common as was *Ribes hirtellum* Michx., while *Dryopteris marginalis* (L.) Gray and *Polystichum braunii* (Spenner) Fee var. *purshii* Fern. were somewhat less frequent. Other pioneers included *Hieracium pilosella*, *Sambucus pubens* Michx., *Epilobium glandulosum* Lehm. and *Diervilla lonicera* Mill.

In all 15 disjunct species have been found at the Indian Brook station, occurring in open or sheltered locations. The little ferns, *Asplenium viride* and *Woodsia glabella*, were restricted to wet, shaded, sheltered crevices and grottoes. On the drier exposed ledges were disjuncts such as *Draba arabisans* and *Achillea borealis* together with common and weedy species. *Saxifraga aizoon* var. *neogaea* persisted on

an exposed, inclined face in acidic soil on acidic rock although it is known as a calciphyte. All three soil samples from this station were slightly acidic.

(B) BIG SOUTHWEST BROOK, INVERNESS CO.

Big Southwest Brook is the main tributary of the North Aspy River which it approaches from the south-southeast. The disjunct station is situated about 1/3 mile upstream from the river, approximately in the centre of the Cape Breton Highlands National Park. The elevation at this point is about 1,000 feet.

To the south the station is delimited by a waterfall, 60 feet high, which tumbles through an extremely narrow and crooked gorge (three to four feet wide in places) into a deep pool below. High cliffs encircle the pool but leave a small rocky bar on the northeast side. Upon leaving the pool the brook runs through a deep, rugged, boulder-strewn gorge. Many of the boulders are 15-20 feet across.

Arctic-alpine plants have been found along cliffs of this brook from the falls to a point approximately ¼ mile downstream. The narrowness of the deep trench through which the brook runs, combined with the orientation of the cliffs, puts the entire station in almost continual shade.

The west wall of the waterfall's narrow channel swings away from the falls to form a huge cliff that towers above the pool. Up to 100 feet high and 120 feet wide at the base this almost sheer cliff is criss-crossed by sloping ledges several feet in width. Wooded hillsides continue upward from the cliff top and also form the northern boundary of this section of the extensive but broken station.

A small pile of rock fragments that obviously had fallen from above was noted in the water at the cliff base but on the whole this face appeared to be fairly stable. Numerous horizontal fractures gave the cliff a stratified appearance. Schist, associated with banded gneiss and white milky quartzite, constitutes the major part of the cliff. Schist, gneiss and quartzite are all acidic rocks; the pH of a soil sample taken from a crevice of this face was 5.6. It should be pointed out here that this cliff previously was thought

to be composed of limestone (Smith and Schofield, 1952), an assumption that seemed quite plausible in the light of the number of calciphytes found upon it.

The entire cliff was extremely wet; water dripped everywhere and in some places it fell down the face in small, continuous streams. Spray from the falls helped to moisten the rock walls but it was chiefly the abundant seepage that created this very wet habitat.

At 0715 hrs. 29th July, the sun first shone on part of the higher region of the cliff, but 30 minutes later shade enveloped the whole face. Other sections of the east-facing cliffs received only a little more direct sunlight. The lack of direct sunlight plus the copious supply of dripping water made these cliffs considerably cooler than the drier, sunlit ones on the east side of the brook.

The commonest species on the waterfall cliff was *Scirpus cespitosus L.* var. *delicatulus* Fern., a boreal disjunct, followed by *Sedum rosea*, an Arctic-alpine plant, and *Thalictrum polygamum*. The first of these three was by far the most common, pioneering the smallest of cracks on the sheer facade. On the many ledges grew other disjuncts, including *Erigeron hyssopifolius*, *Cystopteris fragilis* var. *laurentiana* and *Saxifraga aizoides* L. Also common was *Potentilla fruticosa* L., a species which ranges into the Arctic but is wide-spread in Nova Scotia.

Downstream from the waterfall cliff are other lesser cliffs and overhangs providing habitats for still more disjuncts. *Schizachne purpurascens* (Torr.) Swallen, *Woodsia glabella*, *W. alpina* (Bolton) S. F. Gray, *Solidago multiradiata* Ait., *Draba norvegica* Gunn, *Carex atratiformis*, *Arnica chionopappa* Fern. and *Achillea borealis* were all found in small numbers scattered along the cliffs of this gorge. *Pinguicula vulgaris* L., a species previously unknown for this station was discovered in a wet crevice of a ledge projecting out into the river; only two plants were seen despite a close search. This small population and its dangerous position in time of floods is illustrative of the precarious existence of many of the disjunct cliff-dwellers.

More Arctic-alpine and boreal disjuncts were found at Big Southwest Brook than at any of the other stations studied. It is the only known Nova Scotian station for *Draba norvegica, Saxifraga aizoides* and, above the falls, *Oxyria digyna* (L.) Hill.

The western half of the station generally was wet, well-shaded and thus cool while the opposite cliffs were exposed to sunlight, drier and therefore warmer. The number of disjuncts on the western side was greater, both for total number of species and for total number of plants. The dissimilarity of the two sides is most vividly seen at the falls where the falling water divides the encircling cliff into two distinct vegetational sectors; to the west it is shaded, wet and covered in a lush profusion of higher plants, to the east it is sunlit, dry and covered in lichens. Soil samples from both sides were acidic but the eastern sample was much more acidic than the western.

(C) CHETICAMP RIVER, INVERNESS CO.

One and a half miles southeast of the point where the Cabot Trail crosses the Cheticamp River a steep mountain rises from the south side of the narrow intervale which is but 100 feet above sea level. The western, northern and eastern sides are all very steep but on the south, the top becomes continuous with the flat plateau. An elevation of 1250 feet is reached at the very top, but the cliffs examined had their bases at about the 1000 foot level.

Cliffs encircled much of the topmost region of the mountain with extensive scree beneath them. Some areas were covered by a bare talus, mostly of boulders up to ten feet across. A visit to the station a year after this study was made revealed that almost 1/3 of the former suitable habitat had been swept away by a large slide.

All of the cliff sections investigated were approximately north-facing, very much exposed and usually moist. The first area examined was one of moist dripping cliffs which were quite steep but interrupted by ledges. These ledges were very mossy, supporting *Sedum rosea* and *Potentilla fruticosa*. A wet crevice near the base contained *Scirpus*

cespitosus var. *delicatulus* and *Lycopodium selago* L. *Primula mistassinica* Michx., a boreal-alpine, was frequent on moist ledges near the base.

The second cliff section studied was north-facing and very wet also. Water was continually dripping from the higher regions of the cliffs, splattering on ledges below and finally reaching the ground as a fine spray. When this station was visited the cliff-face habitat was considerably cooler than the intervale below. The slightest breeze was able to blow the falling spray over a wide area of the cliff. Shade provided by the mountain itself prevented rapid evaporation.

A pH of 5.9 was found for a soil sample taken from one of the wet north-facing ledges which supported, among other species, *Achillea borealis* and *Scirpus cespitosus* var. *delicatulus*. The major rock constituent of the cliff proved to be gneiss (an acidic rock), containing quartz, mica and feldspar.

Of the 58 disjuncts considered in this study, eight have been recorded for this Cheticamp River station. Almost exclusively they are found on moist ledges or in damp crevices that abound on the shaded, exposed dripping cliffs.

(D) BIG INTERVALE, INVERNESS CO.

A relatively small disjunct station is located opposite the village of Kingross, on the west bank of the Northeast Margaree River where the river valley widens to form what is known as the Big Intervale. The elevation at the base of the cliffs is approximately 500 feet.

Facing south-east, the cliffs are generally bare and dry, exposed to both the sun and the elements. Scree, stabilized by numerous mature trees, slopes down gently from the cliff base to the flat hay-fields about 50 feet below. The cliffs extend laterally for about 300 yards but are only 50 feet high, at the maximum.

Much of the rock is covered by lichens only but the many ledges enable a number of species to prosper. Most are common weedy species from the fields or from the surrounding forest but ten disjunct species have been recorded

for this small station. On the dry, mossy, exposed cliff *Achillea borealis, Woodsia ilvensis* and *Arabis drummondi* Gray have been able to persist. A small rivulet near the centre of the cliff-face provided the only similarity between this station and the wet, cool shaded habitats of the three stations described previously.

The pH of a soil sample taken from a dry cliff ledge where *Arabis drummondi* and *Woodsia ilvensis* were growing, was 4.6. Rock from this face was described as igneous, probably syenite, which has been highly faulted and fractured. This type of rock is acidic.

(E) HILLSBOROUGH, INVERNESS CO.

On the steep east bank of the Mabou River, one and a half miles upstream from Hillsborough, sheer outcroppings of limestone provide a type of habitat seldom found in Nova Scotia. In the limited area studied — a section of cliff about 60 yards wide by 15 feet high — seepage and small trickles were common, resulting in a generally damp cliff-side. Despite the wet, cool, fairly well shaded habitat only one disjunct species occurs there — *Cryptogramma stelleri* (Gmel.) Prantl. This species, a calciphyte, is known from only one other station in Nova Scotia. Among the non-disjuncts seen were two other calciphytes, *Cystopteris bulbifera* (L.) Bernh. and *Sphenopholis intermedia* Rydb.

(F) LITTLE RIVER, VICTORIA CO.

The cliffs at Little River, about two miles from the Cabot Highway, had not been visited previous to the study. The site was selected at random with the hope that it would present an example of an exposed granitic cliff much similar physically to the disjunct stations. Such was the case. No Arctic-alpine or boreal disjuncts were anticipated on these high cliffs which terminate a long gradual slope from the intervale far below. Part of the lower slope was covered by a huge slide of boulders which evidently had broken from the faces above at some much earlier date since lichens and mosses had become well established. The cliffs were approximately 500 feet above the river level which at this point was 300 feet above sea level. Those faces examined

were from 30 to 50 feet high but were much more extensive laterally.

In general the cliffs were dry and bare but some of the ledges provided anchorage for several species. Trees growing in the stabilized talus gave a measure of shade.

Four disjunct species were found at Little River. *Asplenium trichomanes* L., boreal circumpolar in distribution, occurred frequently on the talus slopes and on the boulder slide. *Dryopteris fragrans* (L.) Schott var. *remotiuscula* Komarov was collected from a small crevice of the sheer cliff. *Lycopodium selago* was fairly common in soil pockets of some of the ledges and *Woodsia ilvensis* appeared to be a pioneer in bare areas. All four were found in slightly acidic soil. None of the really rare disjunct species were seen at Little River.

Soil preferences of a large number of Alpine and subalpine plants were discussed by Fernald (1907). Precipitation and moisture were considered to be of only minor importance in determining the local distribution of these plants in areas south of the St. Lawrence River. A correlation was seen between the distribution of certain species and the presence of limestone and other calcareous rocks. The role of exchangeable calcium in the soil was examined by De Silva (1943) in a study of the distribution of calcicoles and calcifuges. He noted that species which show luxuriant growth on calcareous soils often grow well in soils which appear to have no calcium carbonate whatsoever. Exchangeable calcium was postulated to act as a source of calcium in areas devoid of calcium carbonate.

With the exception of the limestone cliffs at Hillsborough, the stations examined in this study have acidic rock, pH's varying from slightly acidic to strongly acidic and low amounts of exchangeable calcium and magnesium. Most of the species considered here have been described as calciphytes and in the past the local occurrence of such species has often been explained on the basis of calcareous outcroppings. From the present data it would appear that

these plants can also persist where the soil is non-alkaline and even strongly acidic.

Wynne-Edwards (1939) elaborated upon the significance of the type of habitat wherein the Arctic-alpine species chiefly are found. Arctic plants are adapted to exposure and to habitats which undergo great physical change due to the actions of frost and thaw. To the south somewhat similar habitats exist on mountains, cliffs and talus slopes. Those cliffs composed of rocks which yield most easily to the process of weathering come close to resembling, physically, the Arctic habitats. The normal, mesophytic species find such conditions very difficult and often succumb to the competition of the better adapated Arctic-alpine element. The author pointed out that since basic rocks are more pervious and more soluble than acidic rocks they are more easily broken down by the weathering agents. In this way an ever-receding cliff-face and an unstable talus slope are made available to those species which are tolerant of changing, exposed habitats.

Although none of the six stations other than Hillsborough had cliffs of basic rock there was loose rock or talus below all of them. The most stable was probably the main cliff at Big Southwest Brook but even that was much fractured. It seems, then, that acidic cliffs can also provide unstable habitats.

The possible role of microclimate in plant distribution has been discussed by Wolfe (1951). Within the macroclimate of a region there is a complex pattern of microclimates operating just above the substrate and, in some cases, varying considerably from the norm of the region. Wolfe presented climatic data which showed that the maximum temperature for a certain grotto was 18 F. degrees below that of the surrounding countryside. It seems probable that the cooler temperatures of such a shaded habitat could promote the growth of Arctic species which might otherwise fail to survive. Although no temperatures were taken during this study the effect of shade and moisture

was sufficiently pronounced that valid comparisons could be made.

The most productive stations of the six visited in the present project were those which enjoyed the greatest amount of shade and shelter, Indian Brook and Big Southwest Brook. Of the 58 disjunct species 27 were recorded for Big Southwest Brook and 15 for Indian Brook. The cliffs at Cheticamp were moist and cool but were not as sheltered and did not receive as much shade. It is also possible that the almost constant winds at this higher, more exposed site led to faster evaporation. These factors may well in part account for the fact that only 8 species were found on the Cheticamp cliffs.

The Big Intervale station was exposed, very dry and faced southwest. Here only three disjunct species were seen, although in its one hundred years as a known station a total of ten have been reported; perhaps some have failed to survive due to the dry, unshaded environment. The cliffs at Little River were high, exposed, east-facing but quite dry. Only four disjuncts were found there. Although the limestone cliffs at Hillsborough were very moist and fairly well shaded they harbored but one of the 37 disjuncts.

A common denominator for the three most productive stations of this study is a cool habitat. In each case trickling and seeping water was present in varying amounts, moistening the shaded cliffs. The water and the shade are probably not ends in themselves, important though they may be; it is likely that their most important function is in contributing to the coolness of the habitat. The temperature-moderating effect of a river running by a cliff, in combination with shade and seepage, could well be a telling factor in determining the suitability of the habitat for Arctic-alpine species.

While the cool, moist habitat is of great importance it cannot guarantee the presence of disjuncts. If such were the case many of the river valleys and gorges would constitute continuous stations for the Arctic-alpine element. The edaphic and physiographic nature of the habitat also

help to determine which plants will grow there. Exposed, unstable habitats of cliff-faces and talus slopes make the establishment of an individual and the persistence of its progeny very hazardous. But it is on these moist, cool, relatively unstable habitats that the Arctic-alpine element can best compete with the flora of the surrounding areas.

Such habitats are fairly common in northern Cape Breton, present to a lesser extent in the Minas Basin-Bay of Fundy region but only rarely found in other regions of the province; hence, the bicentric pattern of distribution.

Immediately following the retreat of the Wisconsin glaciers the whole of Nova Scotia probably offered habitats suitable for the northern species which, previously, had been pushed south. In the warm period that ensued mesophytic flora took over most of the lowland sites, restricting what are now disjuncts to the cooler localities which were physiographically still pioneer habitats. There the mesophytic flora was at a competitional disadvantage such that the northern species were able to persist although much reduced biotypically due to the rigours of forced migration.

SUMMARY

The peculiar combinations of shade, moisture, temperature, exposure and instability of habitat allow isolated colonies of Arctic-alpine and boreal disjuncts, each typically consisting of a number of species, to exist as biotypically reduced remnants far from the present population centres. These same factors militate against most of the species of the surrounding forest so that the isolated populations can compete on at least an equal basis, thereby maintaining their precarious hold. A minor change in the habitat could swing the competitional balance in the direction of the common species with the almost inevitable elimination of these outliers.

PERRY BIOLOGICAL LABORATORIES,
ACADIA UNIVERSITY, WOLFVILLE, N. S.,
CANADA.

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STUDIES OF THE BYRON BOG IN SOUTHWESTERN ONTARIO XXX. DISTRIBUTION OF ORCHIDS IN THE BOG

William W. Judd

The Byron Bog in London, Ontario has been described by Judd (1957). It shows the zones of vegetation typical of a small black spruce-*Sphagnum* bog (see map, Fig. 1, Judd, 1957, 1966). Zone A is the central portion of the bog and is composed of a floating mat of *Sphagnum* moss almost completely covered by leather-leaf, *Chamaedaphne calyculata* (L.) Moench, and including scattered black spruce and larch trees. Surrounding Zone A is Zone B, a low, wooded area, permanently damp or flooded, and occupied on its inner edge by black spruce and larch and, toward its outer edge, by various deciduous trees and shrubs. The outer zone of the bog is Zone C, an area of comparatively dry, wooded slopes occupied by deciduous trees. In Zone A there is a pond, Redmond's Pond, about two hundred feet long. Further accounts of the vegetation in the zones of the bog are given by Judd (1957, 1966).

The Byron Bog has for many years been of interest to local naturalists, particularly members of the McIlwraith Field-Naturalists' Club, the local natural history club in London, founded in 1890. Before 1961 the bog was in London Township, Middlesex County. In 1961 part of London Township, including the bog, was annexed to the City of London, so the bog is now within the city limits. During its history it has been called by various names. The earlier naturalists called it The Spruce Swamp. It was then successively called Redmond's Swamp (or Redmond's Bog) and Foster's Swamp (or Foster's Bog) after two families of farmers who owned the farm in that part of London Township which included the bog. In more recent years it has been called Byron Bog with reference to the village of Byron, about one-half mile south-west of the bog. This name has been used by staff and students at the University of Western Ontario where research has been conducted on

the bog (Crawford, 1926; Judd, 1957). As will be noted in the following account, the various names used for the bog and mentioned above appear as the localities of collection on labels on herbarium sheets of orchids collected in the bog. In 1966 the bog was acquired by the Upper Thames Valley Conservation Authority as a nature reserve. About half of it was donated to the Authority by the Sifton Construction Company, so the bog is now known officially as the Sifton Bog (Anon., 1967).

Until 1959 the Byron Bog was surrounded for several miles in all directions by farm land and was visited regularly only by interested naturalists. Beginning in 1959, development of land around the bog has proceeded apace, and has been accentuated by annexation of the bog to the City of London in 1961. So to-day the bog is surrounded by subdivisions, schools and a shopping centre and has along its northern limits a major arterial street of London. It is now visited regularly by conducted parties of school children, university students and other groups interested in ecology and nature study. It appears appropriate, then, to record what is known of the distribution of orchids in the bog and to recall observations made during the past on these plants.

An early account of plants collected in the vicinity of London is that of Saunders (1863). In this list he includes thirteen species of orchids, but none of his records indicate that they were found specifically in the Byron Bog. Dearness (1905) published an account of the orchids of Middlesex County and did include references to collections from the bog. Observations on orchids were also made in the bog by members of the Botanical Section of the Entomological Society of Ontario, which existed in London from 1890 to 1904, and are recorded in the minutes of that organization (Anon., 1890-1904). Since 1956 the writer has been engaged in studies of the bog and has published accounts of a few orchids and their periods of blooming (Judd, 1957, 1958). Sheets of specimens of orchids from the bog are in the herbarium of the Department of Botany, University

of Western Ontario (UWO) and of the writer (WWJ). The specimens in the UWO herbarium were collected by local naturalists as far back as 1888, while those in the writer's herbarium were collected starting in 1956 and are referred to by their accession numbers in the following account.

Habenaria lacera (Michx.) Lodd. RAGGED FRINGED ORCHID.

Specimens: Spruce Swamp, *W. E. Saunders,* July 19, 1893 (UWO); Spruce Swamp, *Eli Davis,* July 11, 1934 (UWO); Foster's Bog, *W. G. Colgrove,* July, 1934 (UWO); Byron Bog, *W. W. Judd,* July 21, 1965 (WWJ, 654).

Records: "Mr. Balkwill brought in specimens of — *Habenaria lacera* — from Spruce Swamp" (minutes of meeting of July 5, 1890 (Anon., 1890-1904)); *Habenaria lacera,* Spruce Swamp Bog, *Balkwill* and *McClement,* July 9, 1894 (Plant Records, page 113, (Anon., 1890-1904)).

These five records show that *H. lacera* blooms in the bog during July. On July 21, 1965 when I collected a specimen there were several plants in bloom in the soggiest area of *Sphagnum* moss in Zone A, among the small ponds south of Redmond's Pond. Correll (1950) points out that this species grows in a variety of habitats, including wet sphagnum bogs.

Habenaria psycodes (L.) Spreng. SMALL PURPLE FRINGED ORCHID.

Record: "Mr. Balkwill brought in specimens of — *H. psycodes* — from Spruce Swamp" (minutes of meeting of July 5, 1890 (Anon., 1890-1904)).

No specimens or records are available to indicate in what part of the bog this species was found. It is recorded from a variety of habitats, including *Sphagnum* bogs (Correll, 1950).

Habenaria viridis (L.) R. Br. var. **bracteata** (Muhl. ex Willd.) A. Gray. LONG-BRACTED ORCHID.

Records: "Mr. Balkwill brought in specimens of — *H. virescens* — from Spruce Swamp" (minutes of meeting of July 5, 1890 (Anon., 1890-1904)); *Habenaria virescens,* Spruce Swamp near Hyde Park (Dearness, 1905).

The name *H. virescens,* used in older writings, is shown by Correll (1950) to be synonymous with *H. viridis* var. *bracteata.* No specimens or records are available to indi-

cate in what zone of the bog this plant was found. It is recorded by Correll (1950) from a variety of habitats, including bogs.

Epipactis Helleborine (L.) Crantz. HELLEBORINE.

Specimen: Byron Bog, *W. W. Judd*, August 15, 1966 (WWJ, 722).

Several scattered plants were growing in the shade of deciduous trees on the southwest slopes of Zone C on August 15, 1966. Soper and Garay (1954) show that the earliest record of this species in Ontario was in 1890 and that frequent observations, specially after 1931, have been made of its occurrence since then in parts of southern Ontario with calcareous soils. Its occurrence on the slopes of Zone C in the bog is thus not surprising and permits the addition of Middlesex County to the list of sites occupied by this species.

Pogonia ophioglossoides (L.) Ker. ROSE POGONIA.

Specimens: Spruce Swamp, *W. E. Saunders*, July 19, 1893 (UWO); Foster's Bog, *W. G. Colgrove*, July 19, 1934 (UWO); Redmond Swamp, *L. E. James*, July 9, 1950 (UWO); Redmond Bog, *L. E. James*, June 29, 1952 (UWO, 2 sheets); Byron Bog, *W. W. Judd*, June 23, 1956 (WWJ, 574).

The specimens noted above all bear open flowers and thus indicate that the flowering period in the bog extends from the end of June into July. In 1956 the blooming period was found to be from June 23 to August 6, with maximum bloom occurring on July 2 (Judd, 1958). This is the commonest orchid in the bog and occurs throughout Zone A. On June 30, 1966 several hundred were in bloom in this zone and on July 22 of the same year most of the plants bore seed pods and only four were in bloom.

Arethusa bulbosa L. ARETHUSA.

Specimens: Spruce Swamp, *W. E. Saunders*, June 12, 1891 (UWO); Byron Bog, *W. W. Judd*, June 13, 1956 (WWJ, 570).

Records: *Arethusa bulbosa*, Spruce Swamp, *W. T. Clement*, June 15, 1893 (Plant List, page 96 (Anon., 1890-1904)).

This species grows in the bog in the soggiest parts of the *Sphagnum* mat in Zone A, among the small ponds south of Redmond's Pond. The records indicate that it flowers there

in June. In 1956 its date of maximum bloom was June 18 and of last bloom June 27 (Judd, 1958).

Calopogon pulchellus (Salisb.) R. Br. GRASS-PINK

Specimens: Foster's Bog, *W. G. Colgrove*, July 1934 (UWO); Redmond Bog, *L. E. James*, June 29, 1952 (UWO); Byron Bog, *W. W. Judd*, July 5, 1956 (WWJ, 578).

These records indicate that this species blooms at the end of June and into July. In 1956 the period of bloom began on June 30 and extended to August 3, with maximum bloom occurring on July 6 (Judd, 1958). This species grows in company with *P. ophioglossoides* but is less common and grows more closely against humps of *Sphagnum* than does *P. ophioglossoides* which flourishes on the more open areas of moss. On July 2, 1962 fifty plants were counted in bloom. In 1966, seventeen plants were in bloom in Zone A on June 30, thirty-nine were in bloom on July 8 and on July 22 one plant was in bloom and all others bore seed pods.

Spiranthes cernua (L.) L. C. Rich. NODDING LADIES' TRESSES.

Specimen: Byron Bog, *W. W. Judd*, September 21, 1964 (WWJ, 647).

This was found growing in *Sphagnum* moss in the shade of a close growth of black spruce in the northeast part of Zone B. Correll (1950) records this species from a variety of habitats, including bogs.

Goodyera pubescens (Willd.) R. Br. DOWNY RATTLESNAKE PLANTAIN.

Specimen: Spruce Swamp, *W. E. Saunders*, September 16, 1888 (UWO).

There is no indication of what zone of the bog this specimen was taken in. Correll (1950) records that this species is most abundant in dry or moist coniferous forests. Thus a likely site for growth of this species would have been the southeast part of Zone B where needles from large white pine trees form a layer on the ground. Saunders (1863) records it as common around London in rich woods and Dearness (1905) reports it as "not rare in coniferous woods" in Middlesex County.

Of the nine orchids recorded from the Byron Bog, six are represented by specimens collected in recent years and three, *Habenaria psycodes*, *H. viridis* var. *bracteata* and *Goodyera pubescens*, have not been reported from the bog for several decades. In view of the intensive studies which have been carried on in the last decade and the consequent likelihood that any orchids present would have been noted, it is altogether likely that these latter three are extinct in the bog. It is evident that those orchids which are present are restricted to particular zones.

Zone A — The most prevalent species here is *Pogonia ophioglossoides*, growing generally on the floating *Sphagnum* mat. *Calopogon pulchellus* grows in company with *P. ophioglossoides* but is much less common. *Habenaria lacera* and *Arethusa bulbosa* are in this zone but are restricted to the soggiest parts of the zone among small ponds south of Redmond's Pond. It is likely that *Habenaria psycodes* and *H. viridis* var. *bracteata* occurred in this zone when they were present in the bog.

Zone B — The one orchid found here is *Spiranthes cernua*, growing in moss beneath crowded black spruce trees. It is likely that *Goodyera pubescens* occurred in this zone for, as pointed out previously, it is commonest in coniferous woods.

Zone C — The only orchid found here is *Epipactis Helleborine*, growing on the comparatively dry, but shaded slopes. It is likely that it is relatively a newcomer to the area.

DEPARTMENT OF ZOOLOGY,
UNIVERSITY OF WESTERN ONTARIO,
LONDON, ONTARIO, CANADA.

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CONTRIBUTIONS TO THE FLORA OF BOREAL SASKATCHEWAN[1]

George W. Argus

The flora of boreal Saskatchewan is very poorly known although collections were made there as early as 1819 by Sir John Richardson and in 1827 by Thomas Drummond while these botanists were associated with Sir John Franklin's first and second expeditions respectively. In 1926 the northwestern corner of the province was explored by Hugh Raup and his extensive botanical collections made in the Lake Athabasca area constitute a very important contribution to the botanical knowledge of this region (Raup, 1936). Between 1933 and 1941 the Saskatchewan botanists, W. P. Fraser and R. C. Russell, collected in the southern boreal forest mainly in and around the Prince Albert National Park and in 1950 J. Hudson collected in the Amisk Lake area near Flin Flon, Manitoba. In 1961 there was a renewed interest in the botany of northern Saskatchewan and reports of botanical expeditions have been published

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Map A. The northern 80% of Saskatchewan. Scale: 1 inch equals 80 miles. Dashed line the approximate southern boundary of the boreal forest.

Map B. Detail map of northwestern Saskatchewan. Scale: 1 inch equals 24 miles. 1. William River sand dunes, Lat. 59° 02′, Long. 109° 05′; 2. Little Gull Lake, Lat. 59° 01′, Long. 109°; 3. McFarlane River sand dunes, Lat. 59° 12′, Long. 108° 01′; 4. Yakow Lake, Lat. 59° 12′, Long. 108° 01′; 5. Guts Lake, Lat. 59° 33′, Long. 108° 42′; 6. Stony Rapids, Lat. 59° 16′, Long. 105° 50′.

Map C. Detail map of east-central Saskatchewan. Scale: 1 inch equals 24 miles. The Hansen Lake road is indicated by a dashed line. 7. Candle Lake, Lat. 53° 50′, Long. 105° 18′; 8. White Gull Lake, Lat. 53° 56′, Long. 105° 04′; 9. Lower Fishing Lake, Lat. 54° 03′, Long. 104° 37′; 10. Big Sandy Lake, Lat. 53° 27′, Long. 104° 05′; 11. Limestone Lake, Lat. 54° 38′. Long. 103° 13′; 12 Sturgeon Weir River, Lat. 54° 46′, Long. 102° 35′; 13. Jan Lake, Lat. 54° 56′, Long. 102° 55′; 14. Kistapiskaw Lake, Lat. 54° 50′, Long. 102° 43′.

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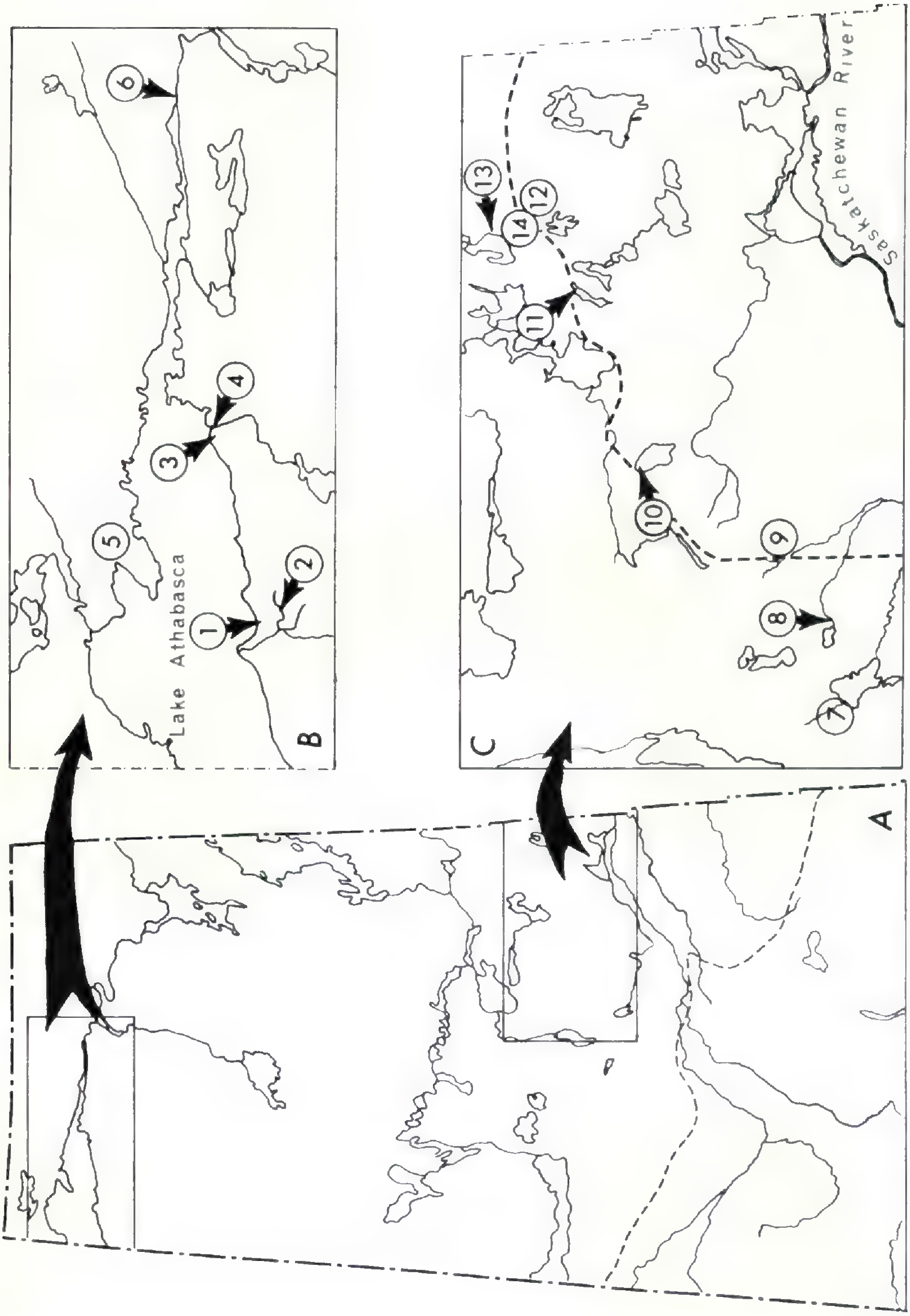
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by Scotter (1961) and Argus (1962, 1964 and 1966). However, in spite of these efforts much of northern Saskatchewan remains botanically unexplored and phytogeographically unknown.

It is the purpose of this paper to comment on 25 new or otherwise interesting unpublished records for boreal Saskatchewan (map A) in order to make this information generally available to taxonomists and phytogeographers. The collections reported here have been made by a number of botanists including J. Hudson, J. S. Maini, M. Swan and the author. All specimens cited here have been deposited in the W. P. Fraser Herbarium (SASK). The collection numbers are the author's unless otherwise indicated. The localities included in this report are plotted on maps B and C.

ISOETES MACROSPORA Dur. Stony Rapids *487-63 and 488-63*. Collections of this species were made on the north and south sides of the Fond-du-Lac River near the settlement of Stony Rapids. The plants were rooted in sand in water 1 to 2 feet deep. Specimen *487-63* was associated with *Subularia aquatica* and specimen *488-63* was growing in a disturbed area used for beaching boats near the Hudson's Bay Company store.

This is the first record of this eastern North American species for Saskatchewan. It was previously reported from Minnesota by Muenscher (1944, map 380) and from northern Manitoba by Ritchie (1959). The specimens were determined by Dr. C. F. Reed.

ISOETES MURICATA Dur. var. BRAUNI (Dur.) Reed. Limestone Lake *4568;* Jan Lake *4691;* Kistapisken Lake *4323*; Little Gull Lake *552-63* and *556-63*. Growing in shallow water, 1/4 in. to 3 feet deep, rooted in sand on lake edges.

Isoetes muricata var. *braunii* apparently occurs throughout northern Saskatchewan on the Precambrian Shield. On the Hansen Lake Road it was not observed in lakes on glacial till but it did appear in Limestone Lake located on Ordovician limestone and was widespread in lakes on the

Precambrian Shield. In northwestern Saskatchewan it was collected in lakes overlying the Precambrian sandstones. Previously it was collected in Saskatchewan by Hudson at Creighton, on the south shore of Meridian Lake, and by Argus (1966) in the northeastern corner of Saskatchewan. The specimens were determined or verified by Dr. C. F. Reed.

ISOETES MURICATA Dur. var. HESPERIA Reed. Sturgeon Weir River *4677*. Growing in shallow water on river's edge; associated with *Elodea canadensis*. A single collection referable to this variety was determined by Dr. C. F. Reed. This is the first record of this variety for Saskatchewan.

NAJAS FLEXILIS (Willd.) R. & S. Big Sandy Lake, *Argus & Hudson 4541*. Rare; growing in water 4 to 6 feet deep on the north side of the lake; associated with *Potamogeton friesii, P. gramineus, P. natans, P. vaginatus, P. zosteriformis* and *Myriophyllum exalbescens*.

This is the first record of this species from Saskatchewan. The American distribution of this amphi-Atlantic species is apparently incompletely understood. Fernald (1929, 1950) describes the species as disjunct in North America with an eastern area extending from Newfoundland to southern Manitoba and a western area in Washington, Oregon and southern British Columbia. Hultén (1958) also maps the species as partially disjunct but includes specimens from the Northwest Territories (just south of Great Slave Lake) and from the North Saskatchewan River at the Saskatchewan-Alberta boundary which partially close the gap between the eastern and western areas. The record reported here from east-central Saskatchewan further fills the gap and suggests that the species may be expected throughout the southern edge of the boreal forest in Saskatchewan, particularly in lakes on glacial till.

FESTUCA RUBRA sens. lat. This circumpolar taxon is highly complex biologically and nomenclaturally and sorely in need of taxonomic revision (see Hultén, 1964, for map and discussion). In northwestern Saskatchewan it is represented by three variants which are outlined here.

FESTUCA RUBRA L. sens. str. McFarlane River sand dunes *773-62*. Growing on the lee slope of a sand dune invading Yakow Lake; associated with *Bromus pumpellianus, Calamagrostis inexpansa, Deschampsia caespitosa* ssp. *beringensis, Elymus mollis* ssp. *mollis, Salix planifolia, Stellaria arenicola* and *Tanacetum huronense* var. *floccosum.*

Specimens referrable to the European *F. rubra* were encountered at Yakow Lake near the eastern end of Lake Athabasca. They differ from the *F. rubra* ssp. *richardsonii* var. *glabrata* in their broader leaves (2 mm broad vs. less than 1 mm broad), taller culms (80 dm tall vs. about 30 dm tall) and longer panicles (9-10 cm long vs. 4-8 cm long).

This species was reported by Raup (1936) from the sand dunes at William Point and from Ennyeuse Creek. I have not seen Raup's specimens and they may represent *F. rubra* or *F. rubra* ssp. *richardsonii* var. *glabrata.*

FESTUCA RUBRA L. var. PROLIFERA Piper. McFarlane River sand dunes *777-62*. Growing with *Festuca rubra* and its associated species.

Only one proliferous specimen of *Festuca* was seen and with the exception of its proliferous florets it looks exactly like *Festuca rubra (Argus 773-62)*. Apparently this variety is new to Saskatchewan (see map 12, of *F. prolifera*, in Porsild, 1966). Raup (1936) cited proliferous forms of *F. rubra* ssp. *richardsonii* (as *F. rubra* var. *arenaria*), however, it is unlikely that this material is the same as *F. rubra* var. *prolifera* for the villous lemmas of ssp. *richardsonii* would immediately separate the two.

FESTUCA RUBRA ssp. RICHARDSONII (Hook.) Hult. *(F. rubra* var. *arenaria).* William River sand dunes *215-62, 403-62, 414-62, 415-62, 507-63, 515-63, 516-63, 567-63, 573-63* and *584-63;* McFarlane River sand dunes *671-62* and *745-62.*

This is an important sand binding species and occurs on active sand dunes or in agrading depressions. On active dunes it is associated with *Bromus pumpellianus, Calamagrostis neglecta, Deschampsia caespitosa* ssp. *beringensis, Elymus mollis* ssp. *mollis, Salix brachycarpa, Stellaria arenicola* and *Achillea millefolium* ssp. *lanulosa* var. *mega-*

cephala. On more stable sites it may be associated with *Agrostis scabra, Calamagrostis neglecta, Arabis lyrata* and *Armeria maritima* var. *interior*.

This subspecies of *F. rubra*, with conspicuously villous lemmas, is very common on the Lake Athabasca sand dunes and was previously reported for Saskatchewan by Raup (193) as *F. rubra* var. *arenaria*.

FESTUCA RUBRA ssp. RICHARDSONII var. GLABRATA Hult. William River sand dunes *227-62, 404-62, 428-62, 429-62, 519-63, 541-63, 568-63, 569-63* and *572-63;* McFarlane River sand dunes *660-62, 661-62, 663-62, 683-62* and *795-62.* This variety of *richardsonii* often occurs with typical ssp. *richardsonii* and may have the same associated species. However, it may occur in more stablized sand dune depressions in association with *Calamagrostis neglecta, Carex aquatilis, Juncus balticus* var. *littoralis, Salix brachycarpa, S. planifolia, S. turnorii, Stellaria arenicola, Arabis lyrata, Empetrum nigrum* and *Armeria maritima* var. *interior*.

The var. *glabrata* is distinguished from the typical variety by its glabrous or merely sparsely pilose lemmas. In this character it resembles *F. rubra* sens. str. but differs as previously described. Populations containing both var. *glabrata* and var. *richardsonii* are common and intergrades are sometimes encountered (cf. *Argus 572-63* and *414-62*).

TORREYOCHLOA PALLIDA (Torrey) Church var. FERNALDII (Hitchc.) Dore. Yakow Lake *806-62*; Stony Rapids, *Maini & Swan 295*. The Yakow Lake collection was growing in wet sand on the lake edge associated with *Ranunculus reptans, Agrostis scabra* and *Equisetum fluviatile*. The Stony Rapids collection was reportedly growing in a "swamp".

This is principally an eastern North American taxon with two disjunct records from western Canada, one from British Columbia and a second from Alberta near the western end of Lake Athabasca (Koyama and Kawano, 1964, map 9A). The collections reported here extend the known range of the species into Saskatchewan and partially fill the gap in the range of var. *fernaldii*. The Yakow Lake specimen was identified by Dr. W. Dore.

CAREX MARITIMA Gunn. William River sand dunes *270-62* and *524-63*. Occurring on gravel barrens ridges within the sand dune complex; associated with *Silene acaulis, Arabis arenicola, Armeria maritima* var. *interior* and *Artemisia campestris* ssp. *borealis.*

This species is rare in Saskatchewan and was seen only twice in the Lake Athabasca sand dunes although it was sought assiduously throughout the area. This is the first Saskatchewan record of this arctic circumpolar species and a southward extension of its range. Porsild (1964, map 78) and Hultén (1964, map 41) show the nearest previous locality for this species to be Great Slave Lake, Northwest Territories.

CAREX MICHAUXIANA Boeckl. Little Gull Lake *491-63*. Growing on a bog island on the north edge of Little Gull Lake; associated with *Sphagnum* spp., *Rhynchospora alba, Juncus stygius* var. *americanus, Arethusa bulbosa, Spiranthes romanzoffiana, Drosera anglica, D. rotundifolia, Sarracenia purpurea* and *Oxycoccus quadripetalus.*

This is the first record of this eastern American species in Saskatchewan. It was previously known as far west as western Ontario (Fernald, 1950) but has not yet been reported for Manitoba.

CAREX OLIGOSPERMA Michx. Little Gull Lake *211-62, 318-62, 338-62* and *500-63*. Growing in *Carex* fens at the edge of bog islands; associated with *Sphagnum recurvum, Scheuchzeria palustris* var. *americanus, Carex limosa, C. rostrata, Eriophorum gracile* and *Smilacina trifolia.*

This is the third report of this uncommon subarctic species for Saskatchewan. It was previously reported from Methye Portage (Breitung, 1957) and from the south shore of Lake Athabasca (Raup, 1936).

CAREX PAUCIFLORA Lightf. Little Gull Lake *353-62* and *588-63*. Growing in *Sphagnum* in open *Picea mariana-Larix laricina* bogs and on a bog island.

This is the first report of this subarctic circumpolar species for Saskatchewan. Previously it was reported from three localities in Manitoba; (1) 50 miles northeast of

Winnipeg (Scoggan, 1957), (2) Reindeer Lake (Baldwin, 1953) and (3) northwest of Lake Winnipeg (Hultén, 1964). The latter locality which appears, on Hultén's map No. 77, to be located in Saskatchewan is actually in western Manitoba because of an error in positioning the Saskatchewan-Manitoba boundary on Hultén's base map.

CAREX TRISPERMA Dew. Little Gull Lake *295-62* and *350-62*. Growing in *Picea mariana-Larix laricina* muskegs and on bog islands along lake edge. The muskeg collection was associated with *Carex aquatilis* and *C. paupercula*. The collection from the bog islands was growing in *Sphagnum* associated with *S. centrale, S. teres, S. warnstorfianum, Aulacomnium palustre, Calliergon stramineum, Drepanocladus unciatus, Carex paupercula, Eriophorum vaginatum* ssp. *spissum, Scirpus hudsonianus, Arethusa bulbosa, Drosera anglica, Sarracenia purpurea* and *Oxycoccus quadripetalus.*

This is the second report of this eastern North American species from Saskatchewan. It was previously reported for Saskatchewan by Hooker (1840) who cited Drummond's collection from Cumberland House. Its occurrence at Little Gull Lake extends its range over 450 miles into northwestern Saskatchewan. Breitung's (1957) citation of this species from Candle Lake, is unsubstantiated because the specimen cited by him could not be located.

ELEOCHARIS NITIDA Fern. Stony Rapids, *Maini & Swan 446*. In a waterlogged roadside ditch.

According to Fernald (1950) this species occurs from Newfoundland to Alaska and south locally to Nova Scotia, northern New Hampshire and northern Minnesota. It is essentially an eastern American species with a small disjunct area in the Western Pacific Coast region of Alaska. The present report constitutes a local occurrence of the species in northern Saskatchewan and is a new record for the province.

RHYNCHOSPORA ALBA (L.) Vahl. Little Gull Lake *492-63*. Growing on a bog island; associated with *Sphagnum* spp., *Carex michauxiana, Juncus stygius* var. *americanus, Are-*

thusa bulbosa, Drosera rotundifolia, D. anglica, Sarracenia purpurea and *Oxycoccus quadripetalus.*

Rhynchospora alba is a boreal species with a more or less disjunct circumpolar distribution (Hultén, 1958, map 249). Its range in North America consists of a large area in northeastern United States and adjacent Canada, a smaller area in the Pacific Northwest and an isolated locality in Alaska. In Saskatchewan the species has been reported from several localities in the aspen parkland and the southern boreal forest (Breitung, 1957). This record extends the range of the species into northwestern Saskatchewan and suggests that the species is to be expected in Manitoba and Alberta thereby closing the gap in its North American range. The identification of *R. alba* was verified by A. E. Porsild.

JUNCUS ALPINUS Vill. ssp. NODULOSUS (Wahl.) Lindm. MacFarlane River sand dunes *786-62.* Found in only one locality growing in a wet depression within the active sand dune complex; associated with *Juncus balticus, Agrostis scabra, Calamagrotis neglecta, Festuca rubra* ssp. *richardsonii* var. *glabrata, Salix brachycarpa, S. silicicola* and seedlings of *S. planifolia* and *S. turnorii.*

This circumpolar species occurs widely in the southern half of Saskatchewan (Hultén, 1964, map 88). This report extends its range into northwestern Saskatchewan. It was previously reported by Raup (1936) from northeastern Alberta and from Great Slave Lake and it is to be expected elsewhere in boreal Saskatchewan.

JUNCUS STYGIUS L. ssp. AMERICANUS (Buch.) Hult. Little Gull Lake *462-62* and *493-63.* Infrequent in *Sphagnum* bogs on the north side of Little Gull Lake. The first specimen was collected on a bog island where it was associated with *Carex michauxiana, Rhynchospora alba, Arethusa bulbosa, Drosera rotundifolia, D. anglica, Sarracenia purpurea* and *Oxycoccus quadripetalus.* The second collection was growing on the inundated margin of a bog island; associated with *Drosera anglica* and seedlings of *Utricularia* sp. (probably *U. intermedia*).

This is the second report of this boreal circumpolar species for Saskatchewan. It was previously reported by Raup (1936) from a slough on William's Point about 13 miles northwest of the locality reported here (Hultén, 1958, map 230).

SILENE ACAULIS L. ssp. ACAULIS var. EXSCAPA (All.) DC. William River sand dunes *272-62* and *528-63*; MacFarlane River sand dunes *690-62*. Forming hummocks on the gravel barrens ridges within the sand dune complex; associated with *Carex maritima*, *Arabis arenicola*, *Armeria maritima* var. *interior* and *Artemisia campestris* ssp. *borealis*.

Silene acaulis and its associated species are restricted to the gravel barrens ridges in the sand dune region of northwestern Saskatchewan. The ridges are covered with a veneer of ventifacts, stones polished by wind-blown sand, and are apparently more stable than other open sand dune habitats. However, the ridges are being slowly degraded and perched specimens of *Salix silicicola* were observed. The species growing on the ridges of the gravel-barrens either have tap roots or are low growing rhizomatous species which are not adapted to agrading dune habitats.

This is the first record of this arctic-alpine, amphi-Atlantic species for Saskatchewan (Hultén, 1958, map 180). The nearest previous location for the species was the eastern arm of Great Slave Lake, N. W. T. (Raup, 1936).

The three specimens cited here have the ciliolate leaf margins characteristic of the species (Hitchcock and Maguire, 1947). However, within the William River sand dunes, plants with non-ciliolate leaf margins are common. As far as I am able to determine, this characteristic is restricted to the Saskatchewan populations and in view of the general endemism which occurs in the Lake Athabasca sand dunes (Raup, 1936) taxonomic recognition of this variant is appropriate. I propose the following name for these populations: **Silene acaulis** L. ssp. **acaulis** var. **exscapa** forma **athabascensis**, forma nov.; differt a specie foliis non ciliolatis; *Argus 529-63* (holotype), *530-63*, *531-63* and *532-63* (SASK). The forma *athabascensis* occurs in the same habi-

tats as the typical form and one specimen *(Argus 272-62)* may be an intermediate having entire and sparsely ciliolate leaves on the same plant.

POLYGONUM VIVIPARUM L. Candle Lake *4906*; White Gull Creek, *Hudson* & *Argus 4395*; Lower Fishing Lake, *Argus* & *Hudson 4416*. The Candle Lake collection was made at Hanin Creek where the species was growing in a very wet *Carex aquatilis-Drepanocladus* fen on the edge of a marly fen. The habitat of the White Gull Creek population was a rich, heavily shaded, stream-side *Salix* thicket including *Salix planifolia, S. pellita, Agropyron trachycaulum, Calamagrostis canadensis, Carex aurea, Stellaria calycantha, S. longifolia, Rubus acaulis, Ribes triste, Halenia deflexa, Mentha arvensis* var. *villosa* and various mosses. The Lower Fishing Lake population occurred in mossy turf along the edge of a lake growing in an open *Salix* thicket adjacent to a *Picea mariana* woods; associated with *Selaginella selaginoides, Equisetum scirpoides, Carex concinna, Zygadenus elegans, Populus balsamifera, Salix bebbiana, S. maccalliana, S. myrtillifolia, S. planifolia, Betula glandulifera, Comandra livida, Silene menziesii, Fragaria virginiana, Potentilla fruticosa, Rubus acaulis, Mitella nuda, Pyrola secunda, Galium septentrionale, Lonicera villosa, Campanula rotundifolia* and *Achillea millefolium*.

This common arctic-alpine circumpolar species was first reported for Saskatchewan from the northeastern corner of the province (Argus, 1966) where it occurred on a boulder field with other arctic species and in mossy turf on a lake edge, a habitat very similar to the Lower Fishing Lake locality. Since that time it unexpectedly has been found in several locations near the southern edge of the boreal forest and is to be expected elsewhere in suitable habitats. Porsild maps a locality in northwestern Saskatchewan (1964, map 130), however, I have not verified this collection.

NYMPHAEA TETRAGONA Georgi ssp. LEIBERGII (Morong) A. E. Porsild. Little Gull Lake *549-64*. An aquatic occurring in a slow moving stream draining Little Gull Lake.

The species is apparently common in this area but flowers late and was overlooked in 1962. The collection cited here was flowering on August 2nd. This is the second record of this species from Saskatchewan. It was previously reported by Breitung (1957) from the Saskatchewan River near Cumberland Lake.

ARABIS ARENICOLA (Richards.) Gelert var. ARENICOLA. William River sand dunes *268-62* and *410-62*. Growing on the ridges of the gravel barrens within the active dune complex; associated with *Carex maritima, Silene acaulis, Armeria maritima* var. *interior* and *Artemisia campestris* ssp. *borealis.*

The specimens cited here agree very well with specimens from the Northwest Territories and Quebec identified as *A. arenicola* except for their glabrous leaves and stems. According to Hopkins (1937) *A. arenicola* consists of two varieties, (1) the typical variety with stems and leaves glabrous and (2) var. *pubescens* (S. Wats.) Gelert, with hirsute stems and leaves. The specimens cited here seem to represent the typical variety which is endemic to the eastern North American Arctic (Porsild, 1964, map 197). A previous collection from the north shore of Lake Athabasca *(Tyrrell 34, 262)*, cited by Raup (1936) as this species is var. *pubescens* (Hopkins, 1937). This report is a notable westward extension of this taxon and is a first record of the species for Saskatchewan.

SUBULARIA AQUATICA L. ssp. AMERICANA Mulligan and Calder. Stony Rapids *489-63*. Growing in mud on north side of the Fond-du-Lac River; associated with *Isoetes macrospora.*

The material cited here has the broad siliques typical of ssp. *americana* (length/width = 1.5) but has the caducous sepals of ssp. *aquatica*. According to Mulligan and Calder (1964) a combination of these characters is common in the cordilleran material they studied and suggests that the Stony Rapids specimens have cordilleran affinities. This is the second record of this uncommonly collected species for

Sasketchewan, the first was collected by Hudson at Amisk Lake (Mulligan and Calder, 1964).

ARCTOSTAPHYLOS ALPINA (L.) Spreng. ssp. RUBRA (Rehder and Wils.) Hult. Candle Lake 4900; Guts Lake, *Maini* & *Swan 565*. The Candle Lake material was collected at Hanin Creek where it was locally abundant in a wet *Picea mariana-Larix laricina* woods; associated with *Aulacomnium* sp., *Selaginella selaginoides*, *Spiranthes romanzoffiana* and *Betula glandulifera*.

This species was previously reported from Charlotte Point, Sasketchewan (northwest of Uranium City) by Raup (1936) and from the northeastern corner of Sasketchewan by Argus (1966). The Candle Lake record is a southerly extension of the Saskatchewan range of this arctic circumpolar species.

PINGUICULA VULGARIS L. Candle Lake *4905*. Growing in a *Larix laricina* fen at the edge of a marly fen; associated with *Drepanocladus* sp. and *Carex aquatilis*.

The occurrence in Saskatchewan of this arctic, circumpolar species has been reported by several authors. The earliest collections were made by W. P. Fraser in a *Carex* fen (calcareous bog) at Prince Albert near the southern edge of the boreal forest. In 1963 it was found in the subarctic northeastern corner of the province (Argus, 1966) and the next year it was discovered at Strawberry Lakes, ca. 50 miles east of Regina, Sasketchewan, well within the prairie zone (Jones, 1964). The specimen cited here was collected about 50 miles northeast of Prince Albert. It is rare in this area where it is restricted to cold, wet calcareous fens.

W. P. FRASER HERBARIUM
UNIVERSITY OF SASKATCHEWAN
SASKATOON, CANADA

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A FLORISTIC COMPARISON OF LOWER CAPE COD, MASSACHUSETTS AND THE NORTH CAROLINA OUTER BANKS

C. JOHN BURK[1]

Cape Cod, Massachusetts, and the Outer Banks of North Carolina are sandy, seaward extensions of the eastern North American landmass which have long been recognized as major points of demarkation in the distribution of marine floras and faunas. The phytogeographic relationships of the vascular floras of these two areas have not, however, been investigated. The purpose of this paper is to compare their modern floras, relating the comparison, so far as possible, to geologic and historical events through the last glaciation to the present, and to evaluate the significance of Cape Cod and the Outer Banks as distributional boundaries for vascular plants. The study is based largely on my own work on the Outer Banks (Burk, 1961) and the recent study of H. R. Hinds (1966) of lower (or "outer") Cape Cod.

Both Cape Cod and the Outer Banks originated, in their present form, as a consequence of the last glaciation, prior to which sea level stood about 25 feet higher than at present, submerging the landmass at both sites completely (Chamberlain, 1964; Richards, 1950). As the glacier formed and moved southward, sea-level dropped from 250 to 360 feet below its present level and Cape Cod was deposited as a series of moraines. Whitehead (1966), evaluating the recent arguments for and against marked displacement of plant community types by the glacier, concludes that a major southward displacement of many boreal species and profound climatic changes can no longer be disputed but that the concept of a zonal displacement of boreal and deciduous forest formations is still open to question.

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At full-glacial time, a continuous coastal plain from Florida to Cape Cod was exposed. At the latitude of the Outer Banks, this plain was an estimated 90 miles in width; its vegetation can be partially reconstructed from palynological studies of the Dismal Swamp, Virginia, and southeastern North Carolina. There are appreciable differences between these two areas (Whitehead, 1966). The forests of Virginia were apparently more boreal in aspect — spruce was possibly the dominant tree and fir was probably not uncommon. In southern North Carolina at this time, red or jack pine (perhaps both) were apparently the dominant species; spruce was much less abundant and fir was very uncommon. A number of northern species including *Lycopodium lucidulum*, *L. annotinum*, *Schizaea pusilla*, and *Sanguisorba canadensis* occurred. It is possible pines were more abundant in this region simply as a result of the prevalence of coarse sands.

As the glacial ice melted, the sea-level rose. The seaward landmass was flooded and the "Provincelands hook" and various sandpits were added to Cape Cod from eroded materials which had previously lain beneath the sea. North of Boston, the level of the initial submergence lies above the present sea level; south of Boston, it is well below (Schafer and Hartshorn, 1966). Hence Cape Cod has not been flooded since the retreat of the glacier; the width of the Cape has, however, diminished markedly. At present, the Great Beach facing the Atlantic is being undermined at a rate of 3 1/2 feet per year (Chamberlain, 1964).

Davis (1965), evaluating various studies of the Pleistocene in northeastern United States, concludes that, following the retreat of the Wisconsin ice, a vegetation floristically similar to sub-arctic vegetation developed in New England. Trees were absent or infrequent for over 2000 years. About 11,500 years ago the climate apparently changed and forest vegetation began to develop in southern New England. Boreal species were abundant at first, with spruce contributing a high proportion of the pollen rain for 2,000 years. By about 8,000 years ago, temperate de-

ciduous trees had become more abundant. There is evidence for a recent interval warmer than the present (Deevey and Flint, 1957; Raup, 1937). Raup suggests that *Chamaecyparis thyoides* may have passed an optimum on the coast and argues that the New England sprout hardwoods are persisting under fundamentally adverse conditions and may, in the normal course of succession, be greatly restricted or replaced by more northerly occurring species.

The greater part of the Outer Banks was created during the period of rising sea-level as a result of local erosion of the sediments of the recently inundated coastal plain by onshore waves. It is not impossible that a few sites on the Outer Banks (most probably, in this writer's opinion, the areas near Nagshead and Cape Hatteras) were exposed throughout this last rise. These sites might then have served as focal points for the subsequent formation of barrier bars and islands and provided refugia for terrestrial plants. The full glacial forests in North Carolina were replaced by forests with abundant oak, hickory, birch, hemlock, beech, elm, and other thermophilous species (Whitehead, 1966); by the close of late-glacial time, the forests were dominated by oak, hickory, and other deciduous species while percentages of hemlock and beech declined. In southeastern North Carolina, an oak-hickory forest type had attained maximum development by early postglacial time, considerably earlier than in southeastern Virginia. Subsequently *Nyssa* and *Taxodium* became more abundant.

There is little evidence to suggest what may have grown on the Outer Banks during the height of the thermal maximum, if such a period existed. Many of the dominant forest species on the Outer Banks persist markedly southward and it is possible that the species composition of the Outer Banks forests was not greatly altered during this time.

Table 1 summarizes climatic data from Cape Cod, the Outer Banks, and inland areas immediately adjacent to each. Cape Cod is colder and to some extent drier than the

Outer Banks; Provincetown has a growing season 89 days shorter than Cape Hatteras, a January average 15 degrees lower, a July average 11 degrees lower, and greater thermal maxima and minima. Both areas have milder climates than areas immediately inland or directly north or south from them.

The sandy soils of Cape Cod are, except for the Provincelands hook and various sandpits, glacial in origin; the sands of the Outer Banks are almost entirely marine. As Boyce (1954) noted, the vegetational structure of the two areas is remarkably similar, a sequence, inward from the open beach, of zonal plant communities from salt-spray tolerant dune grasses and herbs to a tangle of shrubs, vines, and small trees, to a forest which is relatively unaffected by the windborne salt spray. Tidal marshes are common to both areas and, on the Outer Banks, where the bars and islands are separated from the mainland by shallow, more or less enclosed sounds, they are a regular feature of almost any transect drawn from the ocean beach across the bank. On Cape Cod, open salt water brackets the landmass and saltmarshes occur in areas protected by sandspits and in estuaries. Freshwater ponds and pools are more common on Cape Cod as a result of the numerous "kettleholes" formed by the melting glacier.

On the Outer Banks, hurricanes are a major environmental force (Engels, 1952; Burk, 1961). Few hurricanes reach Cape Cod although other storms, primarily winter northeasters (Chamberlain, 1964) may be quite destructive there. Fire is a more important environment factor on Cape Cod than on the Outer Banks.

Much of Cape Cod, unlike the Outer Banks, has been intensively cultivated, and stages of old field succession are relatively common.

FLORISTIC COMPARISON

Neither Cape Cod nor the Outer Banks possess endemic species of vascular plants. The species which comprise their floras range, for the most part, both northward and southward as well as inland, often in different ecological

Table 1. Summary of climatic differences between Cape Cod, the Outer Banks, and inland stations adjacent to each.*

		TEMPERATURE		Degrees F				
Station	Annual precipitation (in.)	January av.	July av.	Max.	Min.	Last spring frost	Earliest fall frost	Growing season (days)
Provincetown (Cape Cod)	39.23	31.6	67.0	104	-8	Apr. 17	Nov. 3	200
Springfield (inland, Mass.)	41.27	27.3	73.2	104	-18	Apr. 27	Oct. 15	171
Hatteras (Outer Banks)	48.59	47.1	78.2	93	8	Feb. 27	Dec. 13	289
Belhaven (inland, N.C.)	50.63	46.0	79.9	106	0	Mar. 29	Nov. 7	223

*Data from U.S.D.A. 1941 Yearbook, *Climate and Man*

Table 2. Native species, genera, families, and orders occurring on lower Cape Cod, the Outer Banks, taxa shared by both areas, and an index of resemblance*.

	Species	Genera	Families	Orders
Lower Cape Cod	586	280	97	42
Outer Banks	462	277	106	43
Shared (both native)	183	170	84	39
Index	39.6	61.4	86.6	92.9

*see text

situations. *Pinus rigida*, for example, a dominant tree in fire-influenced forests on Cape Cod, occurs on similar sites in the New Jersey pine barrens; at the latitude of the Outer Banks, *P. rigida* occurs in the mountains and upper Piedmont only. *Quercus ilicifolia* has a similar pattern of distribution. Distributional data were compiled for all native Outer Banks species from ranges listed in Fernald (1950) and Radford, Ahles, and Bell (1964). Of the 462 native species occurring on the Outer Banks, 418 range south to Florida; 172 range from Maine to Florida; and 23 range north to Maine but not south to Florida. Obviously not all native Outer Banks species which range north to Maine occur on lower Cape Cod, and their exclusion from the Cape Cod flora may be, in large part, accidental.

Any attempt to evaluate the floristic relationships of these coastal areas must consider the relative ease with which plants can become established, thrive, and then quickly disappear on physiographically unstable sites. Changes in the distribution of the stemless palmetto, *Sabal minor*, on the Outer Banks, have been elsewhere recounted (Burk, 1966). Other abrupt changes in the status of various species within the Cape Cod or Outer Banks floras have been noted. Camphorweed, *Heterotheca subaxillaris*, was collected by A. E. Radford from the Cape Hatteras area prior to my own work there. A search of Hatteras Island in 1959 and 1960 yielded no camphorweeds, yet in the spring of 1961 they were found well-established in the vicinity of the Hatteras light, an area which had not been overlooked the year before. The naturalist on the staff of the Cape Hatteras National Seashore reported that camphorweeds, with which he had been previously unfamilar, had first appeared near the Hatteras Light that spring. Camphorweeds also became established on Roanoke Island during that period; they were still persisting in the vicinity of the Hatteras Light four years later. On Cape Cod in the "Provincelands" area near Provincetown, the Christmas fern, *Polystichum achrostichoides*, appeared during the summer of 1966. The station for this fern nearest to the Provincelands is more than 50 miles distant.

Table 2 lists the number of native species, genera, families, and orders found on lower Cape Cod and the Outer Banks, the number of these taxa shared by the two areas, and an "index of floristic resemblance". This index (100 C/N_1 in which C stands for the number of taxonomic units common to the two floras and N_1 is the total number of units in the smaller of the two) is useful because its value is little affected if one flora differs from another in occupying a region of more diverse environments (Simpson, 1965) and should be more widely used in phytogeographic work. Its use in zoogeography is discussed in some detail by Simpson (1943, 1947). The total shared native species represent 132 genera, not all shared genera being represented by the same species in the two areas. Concepts of the various taxa follow Fernald (1950) except in the relatively few instances in which a species lies outside the range of his manual; hence similarities or dissimilarities here noted in the flora basically reflect the presence or absence of taxonomic entities rather than differences in the judgement of taxonomists as to the limits of these entities. Radford, Ahles, and Bell (1964) was consulted for the species outside the range of Fernald.

Cape Cod, with its considerably larger number of species than the Outer Banks, has very nearly the same number of genera and fewer families and orders. The *generic coefficient* (total genera/total species × 100) of Cape Cod is 48; the generic coefficient of the Outer Banks is 60. To some extent, this difference reflects the abundance of polyspecific genera on Cape Cod, their scarcity on the Outer Banks and, in turn, the greater ecological diversity of lower Cape Cod compared with the Outer Banks. Only four Outer Banks genera (*Cyperus, Juncus, Panicum,* and *Quercus*) are represented on the Outer Banks by 8 or more species; 11 genera *(Aster, Carex, Cyperus, Dryopteris, Eleocharis, Juncus, Panicum, Polygonum, Rubus, Scirpus,* and *Solidago)* have 8 or more species on Cape Cod.

Table 3 lists the percentages of the total native floras of Cape Cod, the Outer Banks, and the area of Fernald

Table 3. Percentage of total native floras on lower Cape Cod, the Outer Banks, and the area of Fernald (1950) represented by the three largest families on lower Cape Cod and the Outer Banks and the generic coefficient of each family within each flora.

family	% of total native flora			generic coefficient		
	Cape Cod	Outer Banks	Fernald	Cape Cod	Outer Banks	Fernald
Cyperaceae	11.6	8.0	10.2	16.2	32.4	3.8
Compositae	11.3	13.4	12.7	40.9	48.9	14.5
Gramineae	9.6	14.7	8.8	55.4	58.6	19.3

(1950) represented by Cyperaceae, Compositae, and Gramineae, which are, though not always in that order, the three largest families on both lower Cape Cod and the Outer Banks, and the generic coefficient for each family within each flora. The percentages of the total floras comprised by those families are not greatly different in the three areas. The generic coefficients are markedly higher in the coastal regions than throughout the larger range, reflecting again a greater ecological diversity in the larger range, as well as simply greater area. In all instances, however, the generic coefficient of each family is higher on the Outer Banks than on Cape Cod. The Cyperaceae, with the lowest coefficient in both areas, is the largest of the three families on lower Cape Cod and the smallest of the three on the Outer Banks. Hence, it would appear that ecological diversity, total area, and the relative abundance of families or genera with markedly high or low generic coefficient are factors determining the generic coefficient of any flora. Nonetheless, one would still expect to find increased rates of speciation (and hence a lower coefficient) in more recently assembled floras and lower rates of speciation (and hence a higher coefficient) in older, well-established floras.

Table 4 lists the number of non-native species, genera, and families occurring on lower Cape Cod and the Outer Banks, the number of these taxa shared, and the index of floristic resemblance. Lower Cape Cod has a greater percentage of non-native species in its total flora (20.3%) than does the Outer Banks (17.1%) or eastern United States above Virginia (19.9% in Fernald, 1950). On Cape Cod,

Table 4. Non-native species, genera, and families occurring on lower Cape Cod, the Outer Banks, taxa shared by both areas, and an index of resemblance.*

	Species	Genera	Families
lower Cape Cod	149	110	42
Outer Banks	95	55	33
Shared (both native)	32	38	24
index	33.7	69.1	72.7

*see text

several non-native species including *Rosa rugosa, Artemesia stelleriana,* and *Ammophilla arenaria* are common in salt-spray influenced communities. On the Outer Banks the only well-established non-native species are *Gaillardia pulchella* and *Phlox drummondii,* escaped cultigens found chiefly near habitations.

The non-native floras do not differ greatly from the native floras in their degree of resemblance. This similarity results, in all probability, from the fact that plants tend to become established in areas ecologically not unlike those to which they are native. The origins of the non-native species are summarized in Table 5. The data on the area

Table 5. Percentages of species in the non-native floras of lower Cape Cod and the Outer Banks originating in the Old World, tropical America, and other areas.

	Cape Cod	Outer Banks
Old World (mostly Europe, Asia or Eurasia)	92.5%	81.0%
Tropical America	1.3%	14.7%
Other (Australian, western North America, unknown, tropical cosmopolitan)	6.1%	4.3%

of origin for each species were taken from Fernald (1950) or Bailey (1949). A marked tropical American element present in the non-native flora of the Outer Banks is virtually lacking on lower Cape Cod. The generic coefficient of non-native species on Cape Cod (74) is higher than that of the Outer Banks (61).

An attempt was made to determine the successional community in which the shared species occur. Many of the shared species occur with a rather low degree of fidelity in several communities. However, the greatest number of species common to both Cape Cod and the Outer Banks occurs in the tidal marshes, a fact to which even a relatively casual observer could attest. The dominant forest genera *Pinus* and *Quercus* are represented by different species in each area. On Cape Cod, *Pinus rigida*, *Quercus velutina*, and *Q. alba* are found on drier sites than their counterparts *Pinus taeda*, *Quercus falcata*, *Q. nigra*, and *Q. laurifolia* on the Outer Banks where the rainfall is more abundant. *Fagus grandifolia* occurs in both areas, as do *Acer rubrum* and *Nyssa sylvatica*. *Diospyros virginiana* and *Ilex opaca*, common elements in the Outer Banks forests, are at or near their northern limits on Cape Cod.

Quercus virginiana, a dominant member of the shrub community on the Outer Banks, is tolerant to salt-spray but intolerant to shading and hence usually excluded from the mature forest community. On Cape Cod, *Quercus ilicifolia*, a member of a different subgenus from *Q. virginiana*, occupies a similar niche. On the Outer Banks, *Quercus nigra*, *Q. phellos*, and *Q. laurifolia* form an elaborate hybrid complex (Burk, 1961, 1963) and might well, in that part of their range, be considered one widely-varying species. On Cape Cod, *Quercus velutina* is equally variable; studies have shown that, in part, this variability has resulted from hybridization and introgression with *Q. ilicifolia*. On Nantucket Island, populations of *Q. ilicifolia* show almost certain evidence of introgression with *Q. falcata* which is at its northern limit there (Bicknell, 1909). If forests similar to those in North Carolina were present on Cape Cod during the recent thermal maximum, as they were during other interglacial periods (Dorf, 1960), their replacement by more northerly elements has almost certainly not been catastrophic but rather a gradual exclusion, resulting in relict populations which, while diminishing, often hybridize and introgress with their successors.

CAPE COD AND THE OUTER BANKS AS FLORISTIC POINTS OF DEMARKATION

Dunbar (1958), commenting on W. W. Ashe's statement that coastal or maritime forests could be roughly separated into two divisions at Cape Hatteras, concludes, quite correctly, that "Actually the floral changes are not really very abrupt. As one goes north along the coast, the southern species drop out one by one. Similarly, as one goes southward, the northern species decline. It is interesting, however, that so many of the southern plants are so well represented on the Outer Banks, not far from their absolute northern limit." He lists *Ilex vomitoria, Quercus virginiana, Sabal minor, Tillandsia usneioides,* and *Zanthoxylum clava-herculis* as examples of plants showing this distribution pattern.

The following plant species reach their southernmost point of distribution on the Outer Banks: *Hudsonia tomentosa, Ammophila breviligulata,* and *Juncus articulatus.* The first two of these are prominent in the dune-grass community northward from the Banks. A number of species apparently reach their northern limits on the Banks. These include *Sabal minor, Prunus caroliniana, Smilax auriculata, Yucca aloifolia, Yucca gloriosa, Croton punctatus, Helianthemum corymbosum, Gaura angustifolia, Ludwigia maritima, Hydrocotyle bonariensis,* and *Ipomea sagittata.*

All species whose distributional limits are reached on Cape Cod are southern species at their northern limits, with the exception of *Suaeda richii,* which reaches its southernmost limit on Cape Cod. These include *Diospyros virginiana, Cyperus polystachyos, Juncus biflorus,* and *Spartina cynosuroides.* If Nantucket Island is included as a part of the Cape Cod area, *Quercus falcata, Smilax bona-nox, Lycopodium carolinianum,* and *Ascyrum hypericoides* may be added to this list. A number of species reach their northernmost limit in southeastern Massachusetts in the vicinity of the Cape, including *Quercus stellata, Ilex opaca,* and *Juncus dichtomous.*

The large number of species reaching their northernmost

point of distribution on either Cape Cod or the Outer Banks results, in large part certainly, from the fact that the climates of these areas, as previously noted, is milder than the adjacent mainland. Cape Cod and the Outer Banks are, in effect, northward islands of more southerly climates. If there was a thermal maximum, elements of the floras on Cape Cod and the Outer Banks must be relicts of that period. Relicts from the thermal maximum along the coast north of Boston where the postglacial rise in sea-level covered the present shoreline would have been, in large part, drowned.

SMITH COLLEGE
NORTHAMPTON, MASSACHUSETTS 01060

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CHROMOSOME NUMBERS IN SOME BRAZILIAN COMPOSITAE

James R. Coleman

During the past two decades research on plant chromosome numbers has been increasing at an ever accelerating pace. However as recently as 1963 Heywood and Davis estimated that chromosome numbers had been determined for less than 10% of all species of flowering plants. Even this low estimate gives a somewhat distorted picture of the actual situation since a relatively large portion of northern hemisphere species have been counted whereas there has been a considerable lag in the determination of chromosome numbers of southern hemisphere species.

The Compositae is a convenient and interesting family to investigate cytologically because of its ubiquitous nature and often unsettled taxonomy. The value of chromosome numbers in making taxonomic evaluations and evolutionary interpretations has often been discussed, the most complete recent reference being Heywood and Davis (1963). Also, the fact that the Compositae of North and Central America have been subjected to rather extensive cytological investigation makes further knowledge of South American species especially desirable as it will tend to fill gaps in our knowledge thereby making possible comparisons between taxa occurring in these different areas.

Prior to the present paper, only a single paper (Turner and Irwin, 1960) reporting counts for 14 species had been devoted specifically to chromosome numbers in the Brazilian Compositae. In the present paper counts are reported for 82 individuals representing 68 species distributed amongst 39 genera and 8 tribes. First reports are presented for 6 genera.

MATERIALS AND METHODS

The material examined was collected in the states of São Paulo, Rio de Janeiro and Minas Gerais. A complete set of voucher specimens has been deposited in the herbarium

of the Instituto de Botânica of São Paulo and a nearly complete second set will be deposited in the herbarium of Indiana University.

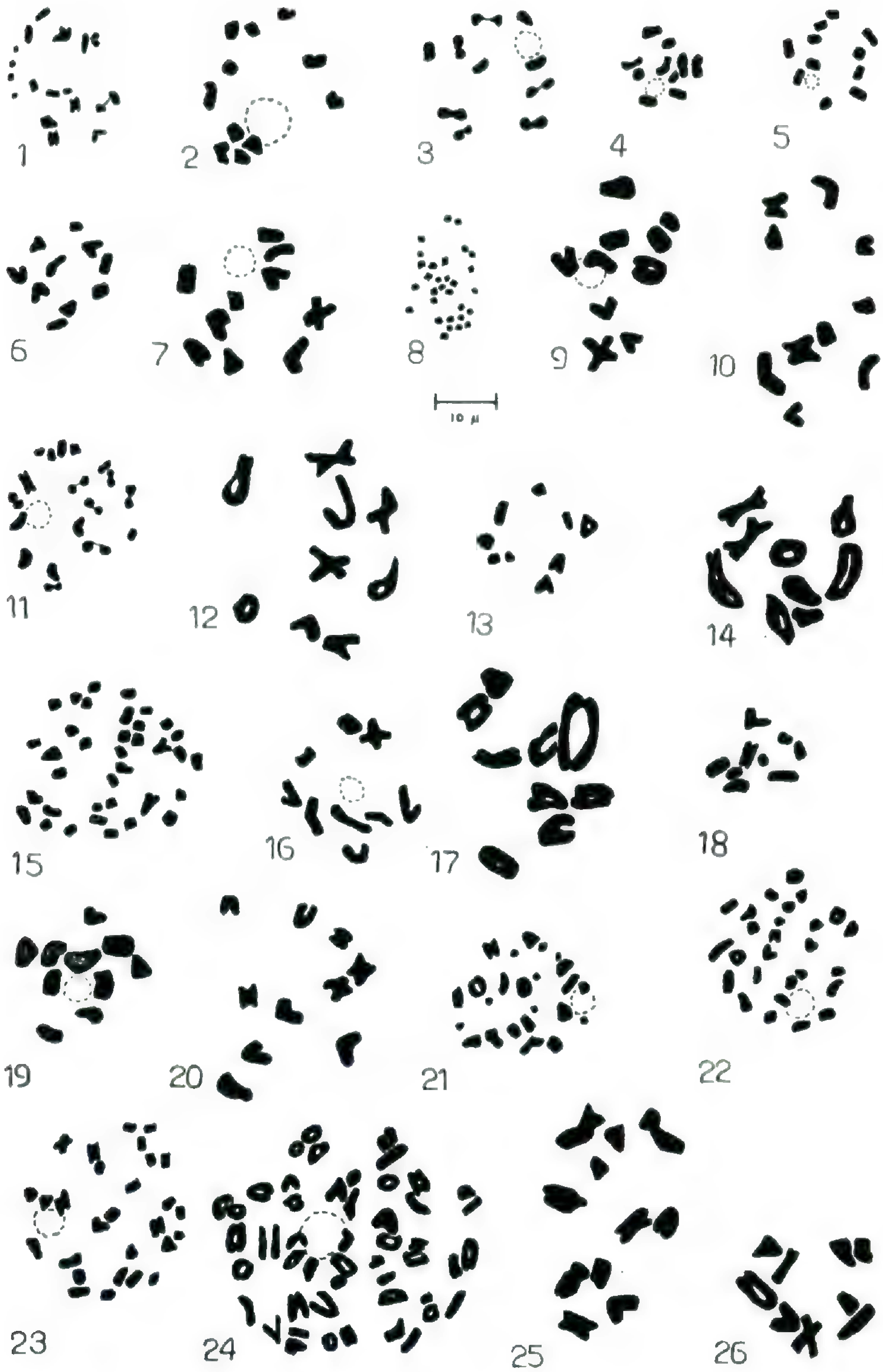
The taxonomic determinations are those of the author, the primary reference being Baker's treatment of the Compositae in Martius' Flora Brasiliensis (1884). Because of the antiquity of this treatment, more recent monographs were consulted whenever possible. In the vast majority of cases material for comparison was available in the herbarium of the Instituto de Botânica of São Paulo.

The buds were fixed in the field in a solution of 6 parts ethyl alcohol: 2 parts chloroform: 2 parts propionic acid and were kept in the fixative for at least 24 hours prior to examination. Immature florets were placed on a slide in a drop of acetocarmine and squashed with a scalpel blade; excess floral tissue was removed and a cover slip applied. The slide was next warmed over an alcohol lamp, inverted on a piece of filter paper and pressed with a steady pressure applied by the thumb. Camera lucida drawings of the chromosomes were made and in many cases slides were made permanent with Hoyer's mounting medium. Selected camera lucida drawings are presented in figures 1-26. Table 1 summarizes the results obtained.

DISCUSSION

VERNONIEAE — The count of $n = 11$ for *Elephantopus mollis* is in agreement with an earler report for this species (Chuang *et al.* in Cave, 1964) from Taiwan. *Orthopappus angustifolius* represents a montotypic genus and the count of $n = 11$ is the initial report of its chromosome number. This species was originally described in the genus *Elephantopus*; however Gleason (1906) considered the pappus characters of this species sufficiently distinct from species of *Elephantopus* to warrant the erection of the monotypic genus *Orthopappus*. The few counts available for *Elephantopus* indicate these two genera to be similar in having $x = 11$. The four species of *Vernonia* reported are in agreement with the majority of previous counts reported for that genus in that they are based on $x = 9$; however each is polyploid.

EUPATORIEAE — *Adenostemma brasilianum* has previously been reported to have $n = 5$ (Turner and Irwin, 1960); however counts reported in the present paper from two populations are $n = 10$. It therefore seems probable either that more than one taxon is involved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in these conflicting reports or that *A. brasilianum* has naturally occurring tetraploid populations. The count of $n = 10$ for *Alomia fastigata* constitutes the second report for that genus. *Alomia microcarpa* (Benth.) Rob. has previously been reported also as having $n = 10$ (Turner and King in Cave, 1965). Three species of *Stevia*, each having $n = 11$, are reported. In addition to counts of $n = 11$, counts of $n = 12$ and 17 have been reported for North American species of *Stevia* (Powell and Turner in Cave, 1964). The count of $n = 10$ for *Trichogonia gardneri* represents the first report for this South American genus of about 25 species, the majority of which are Brazilian. *Symphyopappus cuneatus* and *S. polystachyus*, both $n = 10$, are the first members of that genus to be reported. Robinson (1919) expressed the opinion that *Symphyopappus* is a genus of doubtful value as the characters used to separate it from *Eupatorium* tend to break down. The two species of *Symphyopappus* reported here are similar cytologically to most species of *Eupatorium* thus far reported in having $x = 10$. In the present paper ten species of *Eupatorium*, all based on $x = 10$, are reported. Four species of *Mikania* are reported, each having $n = 18$ or approximately 18. As the bivalents of these species tended to fall apart rather easily, presumably due to low chiasma frequency, exact counts were difficult to secure. The report of $n =$ c. 18 for *Kanimia strobilifera* constitutes the first report for that genus. Hoffmann (1894) placed *Mikania* in the subtribe *Ageratinae* and *Kanimia* in the subtribe *Adenostylinae*. This treatment tends to obscure the evidently quite close affinity of these two genera whose only strong distinguishing character appears to be that the achenes of *Mikania* are 5-ribbed whereas those of *Kanimia* are 8-10-ribbed.

ASTEREAE — The report of $n = 9$ for *Inulopsis scaposa* is the first for this Brazilian genus of perhaps two species. This species was

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FIGURES

1. *Vernonia polyanthes* $n = 18$ 2. *Orthopappus angustifolius* $n = 11$ 3. *Adenostemma brasilianum* $n = 10$ 4. *Alomia fastigata* $n = 10$ 5. *Stevia veronicae* $n = 11$ 6. *Eupatorium intermedium* $n = 10$ 7. *Eupatorium velutinum* $n = 10$ 8. *Eupatorium ballotaefolium* $n = 30$ 9. *Symphyopappus cuneatus* $n = 10$ 10. *Symphyopappus polystachyus* $n = 10$ 11. *Kanimia strobilifera* $n =$ c. 18 12. *Inulopsis scaposa* $n = 9$ 13. *Solidago chilensis* $n = 9$ 14. *Podocoma hirsuta* $n = 9$ 15. *Conyza chilensis* $n = 36$ 16. *Baccharidastrum nottobelidiastrum* $n = 9$ 17. *Baccharis helichrysoides* $n = 9$ 18. *Baccharis oxyodonta* $n = 9$ 19. *Pluchea suaveolens* $n = 10$ 20. *Pterocaulon alopecuroides* $n = 10$ 21. *Clibadium armani* $n = 24$ 22. *Jaegeria hirta* $n = 27$ 23. *Wedelia pilosa* $n = 28$ 24. *Senecio adamantinus* $n = 50$ 25. *Trixis pinnatifida* $n = 11$ 26. *Hieracium commersonii* $n = 9$

included by Baker (1884) in the genus *Leucopsis*, but served as the type species of the genus *Inulopsis* which was erected by Hoffman (1894). Since no chromosome numbers have yet been reported for species undisputedly considered to be *Leucopsis*, no comparison of chromosome numbers between these two genera is possible. The count of $n = 9$ for *Solidago chilensis* concurs with a previous report for this species (Beaudry and Chabot, 1959). *Aster squammatus* has been reported as $n = 10$ (Solbrig *et al*, 1964). In the present paper an approximate count of $n = 9$ or 10 is given. The report of $n = 9$ for *Podocoma hirsuta* is the first report for this genus of about 12 species, the majority of which are South American but two of which are Australian. *Conyza chilensis* has been reported as having $n = 36$ (Solbrig *et al*, 1964) and $n = 36$-38 (Turner and King in Cave, 1965); the count given in the present paper is $n = 36$. The genus *Baccharidastrum* was erected by Cabrera (1937) who distinguished it from *Baccharis* on the basis of the hermaphroditic heads of the former. The count of $n = 9$ for *Baccharidastrum notobellidiastrum* (= *Gonyza notobellidiastrum* Griseb.) is the initial report for the genus. The three species of *Baccharis* reported brings to about 23 the number of species counted in this genus of about 350 species. All reports to date are based on $x = 9$ with polyploidy infrequent.

INULEAE — The report of $n = 10$ for *Pluchea suaveolens* is in agreement with previous reports of other species of this genus. The count of $n = 10$ for *Pterocaulon alopecuroides* is the second report for the genus and the first for a South American species. Turner and Flyer (1966) have reported *P. undulatum* (Walt.) Mohr from Florida also to have $n = 10$.

HELLIANTHEAE — The only previous report for the genus *Clibadium* is for *C. surinamense* L. which is given as $n = 16$ (Turner and King in Cave, 1965). In the present paper *C. armani* is reported to have $n = 24$ which would indicate *Clibadium* to be based on $x = 8$. The haploid complement of *C. armani* revealed a dimorphism in regard to size with 16 larger and 8 decidedly smaller chromosomes (fig. 21). The possibility that the 8 smaller chromosomes are B chromosomes can not as yet be excluded. *Acanthospermum australe* has been reported to have $n = 10$ (Carlquist in Cave, 1959); however the count given in the present paper is $n = 11$. *Acanthospermum hispidum*, the only other member of the genus thus far reported, also has $n = 11$ (Miège in Cave, 1964). *Parthenium hysterophorous* has been reported to have $n = 18$ (Thombre in Cave, 1960), $n = 17$ (DeJong and Longpre, 1963) and $2n = 34$ and 35 (Rollins in Cave, 1963). The count reported in this paper is $n = 17$. The report of $n = 18$ for *Ambrosia polystachya* agrees with a previous report for this species (Turner and Irwin, 1960). *Jaegeria hirta* has been re-

ported three times previously, each as having $n = 18$ (Turner *et al,* 1962; Turner and King in Cave, 1965; Turner and Flyer, 1966). In the present study individuals from two populations were examined, one clearly showing $n = 27$ and the other $n =$ c. 27. The conflicting reports for *J. hirta* suggest either that more than a single taxon is involved or the existence of naturally occurring triploid populations. Species of *Wedelia* have now been reported to have $n = 11, 12, 15, 20, 22, 23, 25, 28, 29 \pm 1$, and c. 36 thus revealing an aneuploid series to exist in the genus. Counts of $n = 16$ and 19 are reported for two species of *Calea.* In addition to counts of $n = 16$ and 19, counts of $n =$ c. 17 and 18 have been reported for North American species (Turner *et al,* 1961; Turner *et al,* 1962).

SENECIONEAE — The count of $n = 10$ for *Emilia coccinea* is in agreement with a previous report for this species (Baldwin, 1946) and the count of $n = 20$ for *Erechtites hieracifolium* concurs with previous reports for this species (Arano in Cave, 1963; Turner and King in Cave, 1965). The counts reported for three species of *Senecio* are consistent with the majority of previous reports for the genus in that they are based on $x = 10$.

MUTISIEAE — Counts of $n = 24$ for *Chaptalia nutans* and *C. integerrima* confirm earlier reports for these species (Turner, 1959; Baldwin and Speese, 1947). Species of *Perezia* have previously been reported to have $n = 8$ (Heiser, 1963) and $n = 12$ (Diers in Cave, 1961). The report of $n = 4$ for *P. cubataensis* establishes that $x = 4$ in *Perezia.* The report of $n = 27$ for *Trixis divaricata* is consistent with previous reports for the genus. However the report of $n = 11$ for *Trixis pinnatifida* indicates *Trixis* to be dibasic with $x = 11$ and 27.

CICHOREAE — Reports of $n = 4$ confirms earlier reports for *Hypochaeris brasiliensis* (Stebbins, 1953) and *H. radicata* (Heiser, 1963; Turner and King in Cave, 1965). *Hypochaeris gardneri,* $n = 5$, is reported for the first time.

SUMMARY

Chromosome numbers are reported for 68 species of Brazilian Compositae, initial reports being made for six genera: *Baccharidastrum, Inulopsis, Kanimia, Podocoma, Symphyopappus* and *Trichogonia. Adenostemma brasilianum,* previously reported to have $n = 5$, is reported to have $n = 10$ and *Jaegeria hirta,* previously reported to have $n = 18$, is reported to have $n = 27$. It is suggested either that more than a single taxon is involved in these conflicting reports or that naturally occurring polyploid populations

exist. It is established that $x = 4$ in *Perezia* and *Trixis* is indicated to be dibasic with $x = 11$ and 27.

DEPARTMENT OF BOTANY
THE UNIVERSITY OF GEORGIA
ATHENS, GEORGIA 30601

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Table 1. List of material examined for chromosome number

Species	$n =$	Locality
VERNONIEAE		
Elephantopus mollis H. B. K.	11	State of São Paulo: Parque do Estado, São Paulo. *190*[2]
Orthopappus angustifolius (Sw.) Gleason	11	State of São Paulo; Parque do Estado, São Paulo. *191*
Vernonia diffusa Less.	c. 18	State of São Paulo: Parque do Estado, São Paulo. *429*
Vernonia polyanthes Less.	18	State of São Paulo: Parque do Estado, São Paulo. *416*
Vernonia scorpioides Pers.	28 ± 1	State of São Paulo: Parque do Estado, São Paulo. *267*
Vernonia cognata Less.	26-27	State of São Paulo: Parque do Estado, São Paulo. *202*
EUPATORIEAE		
Adenostemma brasilianum Cass.	10	State of Rio de Janeiro: Maromba, Parque Nacional de Itatiaia. *369*
Adenostemma brasilianum Cass.	10	State of São Paulo: 13 km SW of Ubatuba. *206*
Ageratum conyzoides L.	20	State of São Paulo: 25 km NE of São Paulo. *295*
Ageratum conyzoides L.	20	State of São Paulo: Parque do Estado, São Paulo. *204*
Alomia fastigiata (Gardn.) Benth.	10	State of São Paulo: Parque do Estado, São Paulo. *374*

[2]Collection numbers are those of the author.

Eupatorium ballotaefolium H. B. K.	30	State of São Paulo: Parque do Estado, São Paulo. *304*
Eupatorium callilepis Sch. Bip.	20	State of São Paulo: Parque do Estado, São Paulo. *428*
Eupatorium congestum H. & A.	20	State of São Paulo: Parque do Estado, São Paulo. *338*
Eupatorium intermedium DC.	10	State of São Paulo: Parque do Estado, São Paulo. *209, 259*
Eupatorium laetevirens H. & A.	10	State of Minas Gerais: Brejo de Lapa, Parque Nacional de Itatiaia. *374*
Eupatorium lanigerum H. & A.	30	State of São Paulo; Parque do Estado, São Paulo. *261*
Eupatorium macrophyllum L.	10	State of São Paulo: Midway between Bertioga and Maresias. *245*
Eupatorium orbiculatum DC.	10	State of São Paulo: 5 km E of São José dos Campos. *282*
Eupatorium pallescens DC.	10	State of Rio de Janeiro: Maromba, Parque Nacional de Itatiaia. *355*
Eupatorium pallescens DC.	10	State of São Paulo: 8-10 km ESE of Campos do Jordão. *346*
Eupatorium vellutinum Gardn.	10	State of São Paulo: 8 km S of Campos do Jordão. *306*
Eupatorium vellutinum Gardn.	10	State of São Paulo: Parque do Estado, São Paulo. *258*
Kanimia strobilifera Gardn.	c. 18	State of São Paulo: c. 5 km E of Itirapina. *260*
Mikania campanulata Gardn.	17-18	State of São Paulo: Parque do Estado, São Paulo. *426*
Mikania capricorni Robinson	17-18	State of São Paulo: Parque do Estado, São Paulo. *427*

Mikania conferta Gardn.	18	State of São Paulo: 8 km S of Campos do Jordão. *181*
Mikania pachylepis Sch. Bip.	18±1	State of São Paulo: Parque do Estado, São Paulo. *291*
Stevia decussata Baker	11	State of Rio de Janeiro: Rebouças, Parque Nacional de Itatiaia. *379*
Stevia conmixta Robinson	11	State of São Paulo: Parque do Estado, São Paulo. *430*
Stevia veronicae DC.	11	State of São Paulo: 8-10 km ESE of Campos do Jordão. *334*
Symphyopappus cuneatus Sch. Bip.	10	State of São Paulo: Parque do Estado, São Paulo. *192*
Symphyopappus polystachyus Baker	10	State of São Paulo: Parque do Estado, São Paulo. *262*
Trichogonia gardneri Gray	10	State of São Paulo: Parque do Estado, São Paulo. *187*
ASTEREAE		
Aster squamatus (Spreng.) Hieron.	9-10	State of São Paulo: Parque do Estado, São Paulo. *314*
Baccharidastrum notobellidiastrum (griseb.) Herter	9	State of São Paulo: Parque do Estado, São Paulo. *196-197*
Baccharis genistelloides (Lam.) Pers.	9	State of São Paulo: Parque do Estado, São Paulo. *387*
Baccharis helichrysoides DC.	9	State of São Paulo: Parque do Estado, São Paulo. *193*
Baccharis helichrysoides DC.	9	State of Minas Gerais: Brejo de Lapa, Parque Nacional de Itatiaia. *376*
Baccharis oxyodonta DC.	9	State of São Paulo: Parque do Estado, São Paulo. *331*

Conyza chilensis Spreng.	36	State of São Paulo: Parque do Estado, São Paulo. *188*
Inulopsis scaposa (DC.) O. Hoffm.	9	State of São Paulo: 8-10 km ESE of Campos do Jordão. *312*
Inulopsis scaposa (DC.) Hoffm.	9	State of São Paulo: 5 km SE of Sao José dos Campos. *317*
Podocoma hirsuta Baker	9	State of São Paulo: Parque do Estado, São Paulo. *230*
Solidago chilensis Meyen.	9	State of São Paulo: Parque do Estado, São Paulo. *290*
INULEAE		
Pluchea suaveolens (Vell.) O. Ktze.	10	State of São Paulo: Parque do Estado, São Paulo. *194*
Pterocaulon alopecuroides (Lam.) DC.	10	State of São Paulo: Parque do Estado, São Paulo. *254*
HELIANTHEAE		
Acanthospermum australe (L.) O. Ktze.	11	State of São Paulo: Parque do Estado, São Paulo. *201*
Ambrosia polystachyus DC.	18	State of São Paulo: 5-8 km E of Amparo. *256*
Bidens segetum Mart. ex Colla	26+2	State of São Paulo: 8 km S of Campos do Jordão. *390*
Calea multipega H. Krasch	16	State of São Paulo: 15 km W of Itirapina. *302*
Calea pinnatifida Banks	19	State of São Paulo: Parque do Estado, São Paulo. *255*
Calea pinnatifida Banks	19	State of São Paulo: 5-8 km E of Amparo. *263*
Clibadium armani (Balbis) Sch. Bip.	24	State of São Paulo: Parque do Estado, São Paulo. *265*
Eclipta alba (L.) Hassk.	11	State of São Paulo: Parque do Estado, São Paulo. *210*

Eclipta alba (L.) Hassk.	11	State of São Paulo: Caraguatatuba State Park. *207*
Jaegeria hirta Less.	27	State of São Paulo: Parque do Estado, São Paulo. *203*
Jaegeria hirta Less.	c. 27	State of São Paulo: 8 km S of Campos do Jordão. *391*
Parthenium hysterophorous L.	17	State of São Paulo: Parque do Estado, São Paulo. *268*
Verbesina glabrata H. & A.	17	State of São Paulo: 13 km SW of Ubatuba. *298*
Verbesina glabrata H. & A.	17	State of São Paulo: Parque do Estado, São Paulo. *297*
Verbesina glabrata H. & A.	17	State of Rio de Janeiro: Rebouças, Parque Nacional de Itatiaia. *382*
Wedelia pilosa Baker	28	State of São Paulo: Parque do Estado, São Paulo. *396*
Wedelia subvelutina DC.	c. 36	State of São Paulo: c. 9 km SW São José dos Campos. *211*
SENECIONEAE		
Emilea coccinea (Sims.) Sweet.	10	State of São Paulo: 10 km NE of Pirassununga. *251*
Erechtites hieracifolium Rafin.	20	State of São Paulo: Parque do Estado, São Paulo. *527, 266*
Senecio adamantinus Bong.	50	State of São Paulo: 8-10 km ESE of Campos do Jordão. *179*
Senecio brasiliensis Less.	20	State of São Paulo: 8 km S of Campos do Jordão. *179*
Senecio erisithalifolius Sch. Bip.	20	State of São Paulo: 8-10 km ESE of Campos do Jordão. *305*
MUTISIEAE		
Chaptalia integerrima (Vell.) Burk.	24	State of São Paulo: Parque do Estado, São Paulo. *309*

Chaptalia nutans (L.) Polak.	24	State of São Paulo: Parque do Estado, São Paulo. *172*
Chaptalia mandoni (Sch. Bip.) Burk.	24	State of São Paulo: Parque do Estado, São Paulo. *285*
Perezia cubataensis Baker	4	State of São Paulo: Parque do Estado, São Paulo. *212*
Trixis divaricata (H. B. K.) Spreng.	27	State of São Paulo: Parque do Estado, São Paulo. *170*
Trixis pinnatifida Less.	11	State of São Paulo: 5 km E of Paranapiacaba. *389*, *397*
Hieracium commersonii Monnier	9	State of São Paulo: 8-10 km ESE of Campos do Jordão. *388*
Hypochaeris brasiliensis Griseb.	4	State of São Paulo: Parque do Estado, São Paulo. *189*
Hypochaeris gardneri Baker	5	State of São Paulo: 8-10 km ESE of Campos do Jordão. *299*, *332*
Hypochaeris radicata L.	4	State of São Paulo: Parque do Estado, São Paulo. *200*

STATUS OF THE GENUS CYMOPHORA (COMPOSITAE)[1]

C. E. ANDERSON AND J. H. BEAMAN

The genus *Cymophora* was founded by Robinson (1907) as a monotypic Mexican member of the tribe Heliantheae. He suggested that it shared many characters with, and appeared to stand near *Eleutheranthera*. The latter was placed in the subtribe Verbesininae by Hoffmann, (1894) and considered distinct from *Aspilia* only in that the asexual marginal florets are lacking or aborted-ligulate. While reviewing various Mexican genera of Compositae, we noted a considerable resemblance between *Cymophora pringlei* and members of the subtribe Galinsoginae, especially certain species of *Tridax*. A detailed comparison (Table 1) of the species with *Eleutheranthera* indicates that these taxa differ strikingly in almost all structures utilized for generic classification in the Compositae, such as the inflorescence, receptacle, phyllaries, pales, anthers, style branches, and achenes. On the other hand, it is so similar to *Tridax* (particularly to *T. accedens*) that there is no basis for retaining it as a separate genus. The following new name is thus required.

Tridax oligantha Anderson & Beaman, nom. nov.

Cymophora pringlei Robins. Proc. Amer. Acad. 43: 39. 1907, *non Tridax pringlei* Robins. & Greenm. Proc. Amer. Acad. 32: 4. 1896. Type: MEXICO. GUERRERO: Iguala Canyon, 2500 ft, 22 Sept. 1905, *C. G. Pringle 10068* (GH, holotype, MSC photo 6732!; MICH, MSC, US, isotypes).

Erect or suberect annual 1.2-4 dm high; stems rather densely pilose and glandular, branched at each node, the principal internodes 6-9 cm long, branches arcuate or flexuous; leaves opposite, the lower on petioles to 1.5 cm long, the upper subsessile, blades broadly lanceolate to ovate, slightly acuminate, green above, paler below, hirtellous

[1]Supported by NSF grant GB-4592. We appreciate the loan of specimens from the U. S. National Herbarium and the Herbarium of the University of Iowa.

TABLE 1. Important features of *Tridax oligantha*, *T. accedens*, *T. dubia*, and *Eleutheranthera ruderalis*.

Tridax oligantha	*Tridax accedens*	*Tridax dubia*	*Eleutheranthera ruderalis*
Inflorescence cymose	Inflorescence cymose	Inflorescence cymose	Heads borne singly in the leaf axils
Receptacle conical, sparsely pilose, knobbed	Receptacle conical, glabrous, knobbed	Receptacle conical, glabrous, knobbed	Receptacle slightly rounded, permanently paleaceous, glabrous, fairly smooth
Phyllaries 6, obovate, convex, margins scarious, 4-8-nerved, pilose and glandular	Phyllaries ca 10, obovate, convex, margins scarious, 4-8-nerved, glabrous to sparsely pilose and glandular	Phyllaries ca 5, broadly ovate to suborbicular, convex margins narrowly scarious, ca 10-nerved, moderately to densely pilose and glandular	Phyllaries 6, narrowly ovate, flat, margins herbaceous, 3-nerved, moderately long-pilose and sessile-glandular
Pales membranaceous, lanceolate-oblong, convex to slightly keeled, 3-5-nerved, deciduous before the phyllaries	Pales membranaceous, broadly oblanceolate, obtuse, convex, 5-nerved, deciduous before the phyllaries	Pales membranaceous, oblong-obovate, subtruncate with a small apiculate apex, convex, 7-nerved, deciduous after the phyllaries	Pales membranaceous below, with herbaceous apiculate apices, oval, convex, 3-nerved, persistent
Heads homogamous, involucre very narrowly campanulate, ca 4 mm high	Heads homogamous, involucre campanulate, ca 4-5 mm high	Heads heterogamous, involucre broadly campanulate, 4-5 mm high	Heads homogamous, involucre campanulate, 5-6 mm high
Florets 10, weakly bilabiate	Florets 30-40 weakly bilabiate	Ray florets 5, disk florets 30-40	Florets 8-10, tubular
Anthers 1.8 mm long, connate, appendages triangular	Anthers 2 mm long, connate, appendages triangular	Anthers 2 mm long, connate, appendages deltoid-ovate	Anthers 0.9 mm long, separate, appendages rounded and scarcely delimited

Achenes black, 2.1-2.3 mm long, narrowly obconical, the outer densely villous, the inner less densely pubescent to glabrate, 5-angled	Achenes black, ca 2 mm long, narrowly obconical, the outer densely villous, the inner pubescent mostly at the base, 5-angled	Achenes black, ca 2 mm long, narrowly obconical, ray achenes moderately pilose, disk achenes glabrate, 5-angled	Achenes brown, 2-3 mm long, turbinate, 3-4-ribbed, sparsely pilose, with warty projections on and between the narrowly winged margins, apex with a mammiform, short-pilose, tubular callous ca 0.7 mm long
Pappus absent	Pappus of ca 20 ciliate scales, in the outer florets 0.5-0.7 mm long, in the inner ca 1 mm long, linear-lanceolate	Pappus of 10 ciliate scales, in the ray florets ca 1 mm long, in the disk florets ca 1.5 mm long, broadly lanceolate	Pappus absent

above and below, 3-nerved from 1-2 mm above the mostly broadly rounded, short-acuminate base, 2-5.5 cm long, 1-3.8 cm wide, margins subentire to serrulate, ciliate; inflorescence a much-branched, many-headed cyme, pedicels 1-2 cm long, filiform, pilose and glandular, the glands reddish on long stalks; heads very narrowly campanulate, homogamous, 10-flowered, 6 mm high, 3-3.5 mm wide; receptacle conical, pilose, knobby, 1 mm wide, ca 0.8 mm high; involucre 2.5-3 mm wide, 4 mm high, phyllaries 6, pilose and glandular, green below, purplish above and near the scarious margins, convex, obovate, 4-8-nerved, striate, 2.5- (outer 1 or 2) 4 mm long, 1-2 mm wide, apex obtuse and somewhat lacerate-apiculate, tardily deciduous; pales ca 7, membranaceous, lanceolate-oblong, 3.8-4 mm long, 0.7-1.2 mm wide, rather obtuse to acuminate-apiculate, subentire, glabrous, convex to slightly keeled, 3-5-nerved, deciduous; ligulate florets absent; outer disk florets 5, corollas minutely glandular and pilose on the purplish tube, minutely pilose near the tips of the white lobes, papillose on the margins, 4 mm long, tube 0.5 mm long, throat 1.8 mm long, the three larger, outer lobes 1.5 mm long, 0.7 mm wide, broadly lanceolate, the 2 smaller, inner lobes 1 mm long, 0.5 mm wide, triangular; inner disk florets 5, similar to the outer but the corollas 3-3.5 mm long with nearly equal lobes; anthers connate, 1.8 mm long, purplish, appendages triangular, bases sagittate; style branches 0.8-1 mm long, elongate, recurved, acuminate-appendiculate; achenes black, narrowly obconical, 2.1-2.3 mm long, 0.6-0.9 mm wide, apex with a low callous ring 0.05 mm high, the outer achenes slightly laterally compressed, densely villous with whitish trichomes (when dry appearing wing-like on the margins) which extend pappus-like from the outside of the apical callous ring, the inner achenes 4-5-angled with the trichomes concentrated on the margins of the inner surface and at the apex, less densely pubescent than the outer.

Additional specimens examined. MEXICO. GUERRERO: 10 mi by gravel road from Tixtla to Chilapa in the arid mts E of Chilpancingo, *Melchert & Sorensen 6145* (IA);

Iguala Canyon, 3000 ft, 2 Oct. 1906, *Pringle 10068 1/2* (MICH, US).

The characters by which *T. oligantha* differs from the closely related *T. accedens* are enumerated in Table 1. Most of these are minor, but it may be noted that the very narrow heads of *T. oligantha*, with 10 florets, in contrast to the more broadly campanulate heads of *T. accedens*, with 30-40 florets, provide a ready means for distinguishing the two species.

Powell (1965) has suggested that *T. accedens* might possibly link *Tridax* with *Galinsoga. Tridax oligantha* might thus appear to provide an even closer approach to that genus. But neither species actually bridges the gap between *Tridax* and *Galinsoga*. Among the characters which ally *T. oligantha* to *Tridax* rather than to *Galinsoga* are the corollas longer than 3 mm, anthers 1.8 mm long, the elongate, appendiculate style branches, and the narrowly obconical, densely pubescent achenes (see Powell, 1965, p. 47 for a tabulation of differences between *Tridax* and *Galinsoga*). The narrow heads might seem to relate it to *Galinsoga*, but the heads are narrow as a result of the few florets. Other species of both *Tridax* and *Galinsoga* have more numerous florets per head. In all aspects except width, the heads of *T. oligantha* are much more similar to *T. accedens* than to any species of *Galinsoga*. Generic status for *T. oligantha* might be argued on the basis of its epappose and eligulate features, but there are other epappose forms in both *Tridax* and *Galinsoga*, and several eligulate species, including *T. accedens*, are known in *Tridax*.

Tridax dubia, *T. accedens*, and *T. oligantha*, respectively, appear to form an evolutionary reduction series. The largest plants, perennial in duration, occur in *T. dubia*, while *T. accedens* and *T. oligantha* are smaller annuals. The heads of *T. dubia* and *T. accedens* have 30-40 florets while those of *T. oligantha* are reduced to 10. Ray florets are present in *T. dubia* and absent in *T. accedens* and *T. oligantha*. The corollas of the disk florets are longer in *T. dubia* than in the other two species. The pappus is longest

in *T. dubia*, shorter in *T. accedens*, and absent in *T. oligantha*. Although *T. dubia* is the basic species in this evolutionary line, it is probably not a very primitive member of the genus.

The morphological similarities of these three species are paralleled by their geographic relationships. Each has a localized distribution on the Pacific slope of southwestern Mexico. *Tridax dubia* occurs near sea level in Colima, Jalisco, and Nayarit at the northwest end of an axis that extends southeast and east through Michoacán to northern Guerrero. *Tridax accedens* occupies an intermediate geographic position, being known only from Coalcoman, Michoacán at an altitude of ca 1000 m. The easternmost member of the three, *T. oligantha*, occurs at about the same altitude as *T. accedens*, and is localized in the Iguala-Chilpancingo region of Guerrero. McVaugh and Rzedowski (1965) have noted that endemism is frequent in southwestern Mexico, and a number of the species of *Bursera* which they studied have distributions corresponding to these species of *Tridax*. In contrast to the evident phytogeographic relationship of *T. oligantha* when associated with *T. accedens* and *T. dubia*, it has no geographic connection with *Eleutheranthera*. The latter is widely distributed in tropical America but has not been reported from Mexico.

DEPARTMENT OF BOTANY, UNIVERSITY OF MICHIGAN,
ANN ARBOR 48104
DEPARTMENT OF BOTANY AND PLANT PATHOLOGY,
MICHIGAN STATE UNIVERSITY, EAST LANSING 48823

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A CYTOTAXONOMIC STUDY OF THE HERBACEOUS SPECIES OF SMILAX: SECTION COPROSMANTHUS*

JOSE K. MANGALY

(Continued from page 82)

TAXONOMY

Smilax L.

Plants dioecious, with annual or perennial shoots from perennial rhizomes, either smooth or armed and terete or angular. Leaves alternate, palmate and reticulate veined, long or short petiolate, petioles often sheathing at base and bearing a pair of tendrils. Flowers in axillary umbels on long or short peduncles, typically trimerous and hypogynous. Tepals 6, usually greenish, with those of staminate flowers larger than those of pistillate flowers. Stamens 6, fixed at the base of the tepals. Anthers oblong, 2-celled, introrse and basifixed. Ovary tricarpellary, syncarpous, superior; stigma solitary or 3, sessile; ovules 1-2 in each carpel, orthotropous. Fruit a berry. Seeds 1-6, with horny endosperm.

Stem annual, herbaceous and smooth,
ovules two in each carpel .... section *Coprosmanthus*
Stem perennial, woody and spinous,
ovules one in each carpel .... sections *Pleiosmilax, Smilax, Macranthae, Coilanthus,* and *China* (woody *Smilax*)

Section *Coprosmanthus*

Smilax section *Coprosmanthus* Torrey, Fl. New York. 2: 303. [1843] 1847.

Nemexia Rafinesque, Neogeneton 3. 1825.

Coprosmanthus Kunth, Enum. Pl. 263. 1850.

Smilax sect. *Nemexia* (Raf.) A. DC. Monogr. Phaner. **1**: 46. 1878.

Smilax Subgen. *Nemexia* (Raf.) Pennell in Bull. Torrey Bot. Club. **43**: 409. 1916.

Rhizome tuberous and perennial, with long thick roots. Stem annual, 1-to many per season, 3 dm to 3 m high, erect or climbing, terete or slightly angular. Leaves few and approximate at top to many and uniformly distributed, alternate; petioles (with sheathing base in some) with a pair of tendrils at the base (absent or with few rudimentary ones in *S. ecirrhata* complex); blades membraneous, ovate to cordate; tip rounded and cuspidate or acute to acuminate. Inflorescences are umbels, 1-to many, on long and slender peduncles, either in leaf axils or in bract axils below foliar leaves; generally one from each node, occasionally three from the same node in one species. Flowers pedicellate, greenish, malodorous in some, trimerous

and hypogynous. Pedicels inserted in small pits on a conical or globose receptacle and slender. Tepals 6, greenish, outer ones generally broader than inner ones, those on staminate flowers larger than those on pistillate flowers, slightly ovate or elliptic to obovate. Stamens 6, reduced and nonfunctional in pistillate flowers, filaments slightly flattened at base, attached at the base of the tepals and free. Anthers oblong, 2-celled, introrse and basifixed. Ovary 3-celled, rudimentary or absent in staminate flowers. Style very short or none; stigmas three, ligulate and recurved. Ovules 2 in each carpel, orthotropous. Fruit a berry, blue to black, with three branches of strengthening tissues running through the pulp connecting the base and apex. Plants flowering generally in early Spring.

KEY TO SPECIES

1. Plants tall, 1 to 3 meters high, climbing; tendrils many, long and functional; peduncles usually many, and from leaf axil.
  2. Leaves pubescent beneath.
    3. Blades dark green, shiny beneath, petiole long; fruits black .... 3. *S. pulverulenta*
    3. Blades light green, not shiny beneath, petioles generally short; berries blue .... 2. *S. lasioneuron*
  2. Leaves glabrous and glaucous beneath.
    4. Pedicels nearly 2× or more as long as the fruit; larger leaves on the main stem broad ovate, not hastate, with 7-9 main veins .... 1. *S. herbacea*
    4. Pedicels more or less equal to diameter of the fruit, larger leaves distinctly hastate, with concave margins, and distinctly cordate base, 3-5 main veins reaching the tip, tip rounded and cuspidate .... 4. *S. pseudo-china*
1. Plants short, up to 1 meter or less in height, erect, with a few short tendrils or none; peduncles few, the lowest one usually from the bract axil.
  5. Leaf blades glabrous and glaucous beneath; leaves few, usually 5-7, approximate at top, cordate at base, tip short acuminate or acute .... 8. *S. biltmoreana*
  5. Leaf blades pubescent beneath.
    6. Basal leaves broadly ovate, base cordate, tip acuminate, petioles generally equal to or shorter than blade .... 6. *S. ecirrhata*
    6. Basal leaves narrowly ovate or elliptical, base mostly ovate.
      7. Leaves approximate at top, tendrils mostly absent, petioles shorter than lamina .... 7. *S. hugeri*
      7. Leaves subverticillate, or equally distributed, progressively smaller and narrowly ovate, tendrils usually many, petioles usually longer than or equal to lamina .... 5. *S. illinoensis*

1. *Smilax herbacea L.*

Smilax herbacea L. Sp. Pl. 2. 1030. 1753.

Type: in Linnaean Herbarium, London, marked by Linnaeus. This specimen was collected by Clayton in Virginia. Linnaeus obtained this specimen evidently from Gronovius and labelled it "*Smilax annua inermis caule fusco purpureo claviculis plurimis teneris vestito. Exalis foliorum oritur pedunculus teres glaber semipedalis gerens flores in capitulos globose, collectors*". This specimen appears to be a duplicate of Clayton's No. 541 now in the Gronovian Herbarium in the British Museum. Both specimens appear to be a small branch characteristically bearing slightly elliptical leaves with pointed tips. These leaves differ from the ovate to slightly cordate leaves expected on the main stem.

S. peduncularis Muhl. ex Willd. in Linn. Sp. Pl. ed. 4: 786. 1806.

Type: Photograph of the type (Willdenow No. 18404, now in Botanisches Museum, Berlin — Dahlem labelled *Smilax "peduncularis . . . habitat in america boreali"*)! Kunth (Enum. Pl. 264) refers to Herb. 18402, but not seen.

Nemexia nigra Raf. Neogeneton 3. 1825.

Used as a new name for *S. herbacea* but, as Pennell points out, it was apparently intended for the black-fruited *S. pulverulenta* Michx.

Nemexia cerulea Raf. 1. c. 3. 1825. Used as a new name for *S. peduncularis* Muhl.

Coprosmanthus peduncularis (Muhl.) Kunth, Enum. Pl. 5: 264. 1850.

C. herbaceus Kunth, 1. c. 265. 1850.

S. herbacea var. *Simsii* A. DC. Monogr. Phan. I: 51. 1878.

Type not seen. Muhl. in h. Willd. fol. 8394. "*S. herbacea* Sims. Bot. Mag. *pl. 1920*". This apparently refers to a narrow-leaved *S. herbacea.*

S. herbacea var. *peduncularis* A. DC. 1. c. 51. 1878.

N. herbacea Small, Fl. S.E.U.S. 2800. 1903.

S. herbacea subsp. *crispifolia* Pennell, Proc. Acad. Nat. Sc. Phil. **62**: 559. 1910.

Type examined. "Herb. Acad. Nat. Sc. Phil. Pennsylvania, Delaware Co. serpentine, Mineral, Sept. 6, 1908. Pennell." This apparently represents a form with narrow, rigid leaves growing in dry and sunny places.

Annual shoots up to 2.5 meters high, climbing and branching; lower cauline leaves narrow and small grading into larger upper leaves (except in younger plants wherein leaves are larger below). Leaves at tip ovate to round, mostly cordate at base. Leaves in general smooth and glaucous beneath, short or long acuminate at tip on the stem and cuspidate on branches; peduncles many on both stem and

branches, axillary to leaves; basal peduncles up to 30 cm long, upper ones progressively shorter. Flowers many in a globose head; tepals greenish, 3.5-4.5 mm long, 1.5-2 mm broad; anthers 1-1.5 mm long, shorter than filaments; style broadly ligulate; fruit about 1 cm in diameter, sub-globose, with 3-6 brownish seeds. Flowering begins in the fourth week of May in the south and extends to the end of June in New England states.

Distribution of *S. herbacea* is mostly along the Appalachian Mountains extending from Georgia and Alabama to Maine and north-eastern Canada. Specimens have been collected from Connecticut, Delaware, Kentucky, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, North Carolina, Pennsylvania, Rhode Island, Tennessee, Vermont, Virginia and West Virginia.

Its closest relative apparently is *Smilax lasioneuron*, a species recognised by many taxonomists as a variety of *S. herbacea*. However, *S. lasioneuron* differs from *S. herbacea* by the pubescence on the leaves and its ecological adaptation to the plains. The smooth glaucous leaf surface of *S. herbacea* is very similar to that of *S. pseudo-china*, which is comparatively smaller in size. *Smilax pulverulenta* is another close relative of this species, but differs from it by the presence of shiny dark green leaf surfaces, pubescence long and mostly on the veins, comparatively fewer flowers on the peduncle, and black fruits.

REPRESENTATIVE SPECIMENS.* ALABAMA. AUBURN CO: *Earle & Baker*, 1898 (F). LEE CO: *Earle & Baker*, May 15, 1898 (RM). CONNECTICUT. FAIRFIELD CO: Stamford, *E. M. Eames*, June 10, 1895 (GH). NEW LONDON CO: Groton, *Janssen*, June 16, 1929 (TEX). DISTRICT OF COLUMBIA. River flat, Chain Bridge, *Pennell* 12072 (PH). GEORGIA. DE KALB CO: Base of Stone Mt., *Mill, Boyd* and *Myres* 481 (GH). HART CO: Wooded bluffs on Savannah R. Smith McGee Bridge, *Harper* 1600 (PH). LUMPKIN CO: Blood Mt., *Leeds* 1560 (PH). KENTUCKY. HARLAN CO: Near summit of Big Black Mt., *McVaugh* 8677, (TEX). MAINE. KENNEBEC CO: Sidney, *Fernald & Long* 13295 (PH). PENOBSCOT CO: Milford, *Fernald & Long* 13296 (GH, PH). PISCATAQUIS CO: Piscataquis River Valley, Dover, *Fernald*, June 6, 1895 (GH). MARYLAND. GARRETT CO: Kelso Gap, Backbone

*Only a partial list of specimens examined is provided here.

Mt., *Core*, June 24, 1931 (WVA). MASSACHUSETTS. BARNSTABLE CO: vicinity of Woods Hole, *J. M. Fogg, Jr.* 1745 (MO). DUKES CO: Gay Head, *Pennell* 3317 (PH). ESSEX CO: Ipswich, *Morong*, June 23, 1875 (NY). HAMPDEN CO: *Seymour* 566 (GH, NY). NORFOLK CO: Milton, *Churchill* 295 (MO). PLYMOUTH CO: *Vail*, July 1888 (NY). WORCESTER CO: near Lancaster, *W. V. Brown*, June 9, 1946 (TEX). NEW HAMPSHIRE. COÖS CO: Shelburne, *Deane*, June 29, 1916 (GH). GRAFTON CO: Lebanon, *G. Kennedy*, Aug. 16, 1890 (GH). ROCKINGHAM CO: Hedge about rich meadows, Rye, *Robinson* 705 (GH). NEW JERSEY. CAMDEN CO: Merchantville, *Meredith*, June 2, 1921 (GH). CAPE MAY CO: Cold Springs, *Pennell* 2200 (MO). MONMOUTH CO: along Big Brook, Marlboro, *Long* 37491 (GH). SOMERSET CO: Watchung, *Moldenke* 2879 (NY). SUSSEX CO: *Britton*, Sept. 28, 1887, (NY). WARREN CO: 2.5 mi. s. of Asbury, *Godfrey* 62142 (FSU). NEW YORK. BROOME CO: Binghamton, *Millspaugh*, 1884 (F). ESSEX CO: shore of Lake Harries, New Comb, *Howe* 10162 (GH). HAMILTON CO: Adirondack Mt. along Hudson River, *Lambert* 22 (NY). New York City: *Edmondson*, June 3, 1899 (NY). ONTARIO CO: *Hall*, 828-1834 (F). ST. LAWRENCE CO: Narros Island, Blake Lake, *Fernald, Wiegand & Eames* 14219 (GH). TOMPKINS CO: South Hills, Ithaca, *Thomas* 2018 (GH). ULSTER CO: vicinity of Lake Mennewaska, *Sowden*, July 3, 1922 (PH). WESTCHESTER CO: Bedford Hills, *Pennell* 7085 (PH). NORTH CAROLINA. ALLEGHENY CO: 1.7 mi. n. of Amelia, *Radford* 34093 (NCU). ASHE CO: 0.6 mi. s. of Warrensville, *Radford*, Aug. 1, 1958 (NCU). BURKE CO: Tim's Creek, east of Drowning Creek Mt., *Bell* 6518 (NCU). DAVIDSON CO: Ellis Creek, about 2 mi. e. of Newsome, *Ahles* with *Haesloop* 57412 (NCU). GUILDFORD CO: Greensboro, *Causey* (NCU). HAYWOOD CO: Piney Mt., *Coker*, July 31, 1926 (NCU). JACKSON CO: 1 1/4 mi. s.w. of Balsam, *Radford*, June 26, 1946 (NCU). MADISON CO: 7.4 mi. n. of jct. U. S. 19 and 23 on U. S. 23, n. of Mars Hills, *Ahles*, with *Duke* 46324 (NCU). MONTGOMERY CO: 1.3 mi. w. of Eldorado on N. C. 109, *Ahles* with *Haesloop* 57346 (NCU). ORANGE CO: Chapel Hill, *Radford & Steward* 650A, (NCU). POLK CO: Tryon, *Peattie* 1173 (NCU). ROWAN CO: 3 1/2 mi. n.w. of Cleveland, *Ahles* 12980 (GH). SWAIN CO: Andrews Bald Ridge, Great Smoky Mt. Nat. Park, *Sharp & Jennison* 585 (TENN). TRANSYLVANIA CO: Glaucester, *Memminger*, Sept. 20-30, 1895 (NCU). YANCY CO: 3 mi. n. of Burnsville, *Radford*, July 9, 1946 (NCU). WILKES CO: 4 1/2 mi. n.w. of Vashti, *Radford* 13718 (NCU). PENNSYLVANIA. BEDFORD CO: 1 1/2 mi. n. ne. of Grand View, *Berkheimer*, July 8, 1939 (MO). BUCKS CO: Hedgerow, 2 1/2 mi. n.w. of Neshaminy, *McDowell* 267 (GH). CARBON CO: 1 mi. s. se. of Little Gap Village, *Wherry*, June 13, 1952 (PH). CENTRE CO: Bear Meadows, *Leeds* 1405 (PH). CHESTER CO: Nottingham Barrens, *Pennell* 1421 (MO). CLARION CO: 1 3/4 mi. s. of Sligo, *Wahl* 18790 (FSU). DELAWARE CO: *Pennell*, July 5, 1905 (F). ELKS CO: 3

mi. w. of Ridgeway, *Westerfield* 2159 (GH). JEFFERSON CO: 1 mi. n.e. of Summerville, *Wahl* 3593 (GH). MONTGOMERY CO: near Sumneytown, *Leeds* 1956 (MO). NORTHAMPTON CO: Fallowfield, 1 mi. e. of Lower Saucon, *Schaeffer, Jr.,* 5069 (GH). PERRY CO: above Marysville, *Small,* June 18, 1888 (F). WARREN CO: Heart's Content, Allegheny National Forest, 20 mi. s. of Warren, *Pennell* 26613 (PH). WESTMORELAND CO: *Block,* June 1881 (LCU). YORK CO: *Britton,* July 2-6, 1904 (NY). RHODE ISLAND. NEWPORT CO: north of Crescent Beach, Block Island, *Fernald, Long & Torrey* 9249 (GH, PH). PROVIDENCE CO: Providence, *Thurber,* June 1844 (GH). SOUTH CAROLINA. DARLINGTON CO: at Lauthers Lake, *B. E. Smith* 9, (NCU). OCONEE CO: *House* 2119 (US). TENNESSEE. COOKE CO: along Highway 75, near Cosby, *Raper & Jenison* 3383 (TENN). HENDERSON CO: near Club Lake, moist slope, Natchez Trace State Park, *Sharp, Fairchild, E. Clebsch & A. Clebsch,* July 8, 1948 (TENN). MONROE CO: moist slope along Sycamore River Gorge, *Gillespie, Laing & Sharp* 18846 (TENN). VERMONT. ADDISON CO: Middlebury, *Brainerd,* June 1877 (GH). BENNINGTON CO: Manchester, *Day,* Aug. 30, 1898 (GH). WINDHAM CO: banks of Corn River, Westminster, *Robinson* 4, (GH). VIRGINIA. APPOMATTOX CO: 8 mi. n.w. of Pamplin City, *Kral* 11215 (NCU). BLAND CO: Dismal Creek, near Giles Co. line, *Potter,* July 12, 1936 (NCU). BOTETOURT CO: along Bearwallow Creek, below Gap, *Freer* 1602 (GH). DINWIDDIE CO: east of Burgess Station, *Fernald & Long* 9898 (GH). FAIRFAX CO: Great Falls, *Pennell* 1670 (NY). GILES CO: west side of Mt. Lake, *Kral* 9176 (FSU). GRAYSON CO: Troutdale, *Gleason,* June 21, 1940 (NY). MONTGOMERY CO: 1.5 mi. s. of Ellett, *Kral* 9176 (FSU). PAGE CO: Stony Man Mt. and vicinity in the Blue Ridge, near Luray, *E. S. Steele & Mrs. Steele* 176 (GH, NY). PULASKI CO: along Peak Creek on Peak Mt., *Small,* July 16, 1892 (GH, MO). Richmond: University Campus, *Angus* and *Haywood* 4471 (GH). SHENANDOAH CO: Valcour, *Pennell* 12119 (PH). SMITHE CO: northwest slope of Mt. Rogers, *Ramseur* 4402 (NCU). SOUTHAMPTON CO: along Three Creek, n.w. of Carey Bridge, *Fernald & Long* 10204 (GH). SUSSEX CO: along Nottoway River, s.e. of Homeville, *Fernald & Long* 10203 (GH). WEST VIRGINIA. BARBOUR CO: 1 mi. n. of Kasson, Rt. 92, *Haller,* June 5, 1951 (WVA). BRAXTON CO: Sugar Creek, s. of Grassaway, *Boggs,* June 29, 1953 (WVA). CALHOUN CO: Grantsville, *Harris,* July 1, 1933 (WVA). MERCER CO: Oakvall, Mtn., *McNeill,* May 30, 1931 (WVA). MONONGALIA CO: *Millspaugh* 63 (WVA). OHIO CO: Wheeling Girls Scout Camp, woody hillside Middle Wheeling Creek, *Bartholomew,* July 22, 1934 (WVA). PENDLETON CO: Spruce Knob, *Rydberg* 9175, (NY). POCAHONTAS CO: along U. S. 250, 2 mi. n. of Durbin, *Clarkson* 3956 (WVA). PRESTON CO: Cheat River near Kingwood, *Core,* Aug. 1, 1931 (WVA). TUCKER CO: *Sharp,* July 18, 1940 (WVA). TYLER CO: along Tygarts River, 2 mi. n. of Crafton, *Core*

5496 (WVA). WEBSTER CO: *Hinkle*, Aug. 1957 (WVA). WETZEL CO: thickets at north of Sugar Run, 1 1/2 mi. w. of Littleton, *Haught* 407, (WVA). WRIT CO: on shady bank of Little Kanawha River, about 3/4 mi. above mouth of Reedy Creek, *Bartholomew* W-1312 (WVA).

2. *Smilax lasioneuron Hook.*

Smilax lasioneuron Hooker, Fl. Bor.-Am. 2: 173. *Pl. 187A*. 1840.
Type: Royal Bot. Garden, Kew, "Hab. Carlton House, Fort on the Saskatchewan, Dr. Richardson"!

Coprosmanthus lasioneuron (Hook) Kunth, Enum. Pl. 5: 265. 1850.

S. herbacea var. *lasioneuron* A. DC., Monogr. Phan. 1: 52. 1878, *synonym*.

S. herbacea var. *inodora* M. E. Jones, Bot. Gaz. 4: 248. 1879.
Type not seen.

S. diversifolia Small, Bull. Torrey Bot. Club. **25**: 607. 1898.
Type: Herb. Columbia University at NY, collected along the Flint River near Albany, Ga., J. K. Small. Apparently same as *S. lasioneuron* Hook!

S. tenuis Small, Bull. Torr. Bot. Club. **25**: 607. 1898.
Type seen. Herb. of Columbia University at the New York Bot. Garden. "The original specimens were collected by Dr. Hale, many years ago in Louisiana". This is taken to be a depauperate young specimen of *S. lasioneuron* Hook.

Nemexia tenuis Small, Fl. S.E. U.S. 281. 1903.

N. herbacea var. *melica*. A. Nelson, Proc. Biol. Soc. Wash. **17**: 175. 1904.
Type not seen.

N. lasioneuron (Hook.) Rydb. Bull. Torr. Bot. Club. **32**: 610. 1905.

Shoots 2-2.5 meters high and branching. Basal cauline leaves narrow and small; larger leaves above, short petioles, ovate to round, mostly cordate at base, pubescent below and margin convex, tips acuminate to round and cuspidate: younger plants with larger leaves below: the transition between leaves and bracts is abrupt. Peduncles many on stems with a few occasionally on branches, axillary to leaves, generally short, with many flowers in a globose head at tip. Tepals greenish, 3.5-4.5 mm long, 1.5-1.75 mm broad. Anthers 1.5-2 mm long, generally equal to or shorter than the filaments. Fruit a subglobose berry, dark blue, glaucous, with 3-5 seeds. Flowering begins in the second week of May and reaches its peak in the fourth week in the south; about 2 weeks later in the north.

Distribution is mostly in the central plains and lower elevations of the Appalachian and Rocky Mountains. In the northern and western drier areas, plants are shorter than those in the southern humid areas. Plants have been collected from Alabama, Arkansas, Colorado, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Michigan, Minnesota, Missouri, Montana, Nebraska, New York, North Dakota, Ohio, Oklahoma, Pennsylvania, South Dakota, Tennessee, West Virginia, Wisconsin and Wyoming.

Its closest relative appears to be *Smilax herbacea*. Apart from its ecological adaptation to lower elevations and drier conditions, the only easily recognisable morphological difference is the presence of pubescence on the leaves in *S. lasioneuron*. The much-emphasised shorter peduncle in this species is a highly fluctuating character. Specimens from central Canada (the type specimen was collected from this region) show greater uniformity in this character, but in the humid southern regions of central United States, the peduncles are generally long.

There is considerable morphological variation in *Smilax lasioneuron* populations in western Florida, especially along Chippola and Appalachicola Rivers. Two other species, *S. hugeri* and *S. biltmoreana*, are also found in the same general area. Intermediate forms of these species are found in herbaria. I feel, therefore, that it is safe to assume that there is some amount of hybridization between all combinations of these species in this general area.

REPRESENTATIVE SPECIMENS: ARKANSAS. BENTON CO: Sulphur Spring along Butler Creek, *Pennell* 5366 (PH). FULTON CO: Mammoth Springs, *Pennell* 11563 (PH). LOGAN CO: top of Magazine Mt., *Pyle* 555 (TEX). COLORADO. BOULDER CO: near Boulder, *Ramaley* 2612 (RM). LARIMER CO: along Buckhorn Creek, *Osterhout*, June 24, 1897 (RM). Horsetooth Gulch, *Crandall* 2438 (RM). FLORIDA. GADSDEN CO: Chattahoochee, *Godfrey* 54563 (GH). GEORGIA. BURKE CO: woods facing the Shell Bluff on Savannah River, N. Leeds, *Harper* 2749 (PH). DE KALB CO: *Eggert*, May 23, 1897 (MO). ILLINOIS. CHAMPAIGN CO: *Gates* 2020 (MICH). COOK CO: west shore of Lake Michigan, Glencoe, *Churchill*, July 26, 1926 (MO). DU PAGE CO: Glen Elbyn, *Shaughnessy* 109, (WIS). JACKSON CO: Big Muddy and Crab Orchard Creek, *McGee Jr.*, 778 (MO). JO DAVIESS CO: east of Apple River

Canyon State Park, *Koelling* 423 (TENN). JOHNSON CO: Reevesville, *Palmer* 15354 (MO). KANKAKEE CO: near the mouth of Rock Creek, *Jones* 15888 (MO). LAKE CO: *Gates* 3115 (MICH). LA SALLE CO: Starved Rock, *Greenman, Jansing Jr., & Dixon* 118 (GH). MC DANOUGH CO: *Kauffman* 204, (MICH). MENARD CO: Athens, *Hall,* 1861 (GH). PEORIA CO: *Stewart,* July 2, 1869 (F). STARK CO: along Mud River, *Chase* 1608 (MICH). ST. CLAIR CO: *Eggert,* May 13, 1896 (MO). UNION CO: Wolf Lake, *Fuller* 595 (WIS). INDIANA. ALLEN CO: west end of Preglacial Lake Maumee, *Friesner* 20388 (GH). CLINTON CO: *M. Ek,* July 4, 1942 (MO). HARRISON CO: along Mosquito Creek, about 3 mi. n. of New Boston, about 4 mi. e. of Laconia, *Deam* 63685 (FLAS). MONTGOMERY CO: *Ward,* Aug. 26, 1944 (FLAS). POSEY CO: in a low wood about 2.5 mi. s.w. of Hovey Lake, *Deam* 24325 (A). SULLIVAN CO: woods near Paxton, *McCoy* 3791 (FSU). WAYNE CO: Earlham, *Pennell* 9819 (PH). WHITE CO: small island in Freeman Lake, *Ward,* Aug. 22, 1945 (FLAS). IOWA. BOONE CO: Cass Twp. 5 mi. s.w. of Luther, along Des Moines River, *Hyden* 8508, (NY, MO). DECATUR CO: *Anderson,* June 25, 1904 (RM). DICKINSON CO: West Okohaji Lake, *Shimek,* June 12, 1916 (WIS). EMMET CO: Esterville Twp., *Hyden* 3031 (GH). FAYETTE CO: *Fink,* June 1894 (GH). JOHNSON CO: *T. J. Fitzpatrick & M. F. L. Fitzpatrick* (F). PLATO ALTO CO: eastern shore of Lost Is. Lake in Lost Is. Park, *Hyden* 8510 (TEX). KANSAS. ATCHINSON CO: 3 mi. n.w. of Atchinson, *Sr. Jeanette,* July 18, '36 (LCU). DONIPHAN CO: 1 mi. s.e. of Iowa Point, *Horr* 4477 (GH). LINN CO: *Bush* 15502 (MO). RILEY CO: *Norton* 515 (GH, MO, NY, RM, US). WILSON CO: near Neodasha, *Palmer* 21385 (A). WYANDOTTE CO: Rosedale, *Mackenzie,* July 12, 1892 (NY). KENTUCKY. NELSON CO: Samuels, *Sr. Agnes* 1522 (LCU). MICHIGAN. BERRIEN CO: New Buffalo, *Lansing* 3290 (F, GH, WIS). MONROE CO: 2 mi. s.e. of Milan, *Robertson* 384 (MICH). ST. CLAIR CO: near Port Huron, *Dodge,* June 18, 1893 (MICH). ST. JOSEPH'S CO: Mendon, *Umback* 7642 (MICH). WASHTENAW CO: n. of Ann Arbor, *Ehlers* 3792 (MICH). WAYNE CO: *Farwell* 9080 (MICH). MINNESOTA. HENNIPIN CO: Spring Grove, *Rosendahl,* June 6, 1902 (GH). OLMSTEAD CO: 2 mi. s. of Morion, *Butters, Moore & Schultz* 7562 (LCU). ST. LOUIS CO: 1 mi. w. of Cotton, *Lakela* 6907 (WIS). MISSOURI. ADAIR CO: 6 mi. n. of Novinger, *Palmer & Steyermark* 4114 (MO). CASS CO: *Broadhead,* June 7, 1864 (MO). CLARK CO: near Dumas, *Palmer* 21864 (A). CRAWFORD CO: 4 mi. s. of Bourbon, *Bauer* 225 (F). DALLAS CO: 2.5 mi. n.w. of Junas, *Steyermark* 24205 (MO). FRANKLIN CO: *Pammel,* June 25, 1898 (MO). GREEN CO: along U. S. 66, e. of Springfield, *Henderson,* May 10, 1959 (FSU). HOLT CO: above Missouri River, near Forest City, *Palmer* 25394 (A). HOWELL CO: 8 mi. w. of Burnham, *Steyermark* 23540 (MO). JACKSON CO: Independence, *Bush* 719 (MO). JASPER CO: near Forest Hill, *Palmer* 18371 (GH). JEFFERSON CO: *Eggert,* July 15, 1892 (MO).

Ditmar, *Kellog* 1660 (MO). LAFAYETTE CO: 1 mi. n. of Chapel Hill, *Steyermark* 24699 (MO). MADISON CO: *Steyermark* 71206 (F). MARION CO: near Taylor, *Palmer & Steyermark* 40650 (MO). MERCER CO: 3 mi. s. of Linesville, *Palmer & Steyermark* 41302 (MO). NEWTON CO: George Washington Carver National Monument near Diamond, *Palmer* 62804 (WIS). OZARK CO: *Steyermark* 22800 (MO). PIKE CO: *Davis* 4172 (MO). POLK CO: near Gydon Springs, *Palmer* 29022 (A). ST. LOUIS CO: Allenton, *Letterman*, June 7, 1898 (MO, NY). TEXAS CO: 3 mi. w. of Houston, *Steyermark* 15537 (MO). WEBSTER CO: 3 mi. w. of North View, *Palmer* 60209 (F). MONTANA. ROOSEVELT CO: Calais, *Blankinship*, July 14, 1900 (MO). NEBRASKA. CHERRY CO: *Tolstead* 105 (GH). LANCASTER CO: Lincoln, *Hedgcock*, May 22, 1900 (TEX). NANCE CO: 4 mi. n. of Fullerton, *Osborn* 1200F (MO). SHERIDAN CO: 13 mi. n. of Haysprings, *Nixon* 81 (RM). THOMAS CO: Emerson Lake, *Kiener* 20061 (F). NEW YORK. OSWEGO CO: near Cleveland, *House* 15937 (GH). NORTH DAKOTA. BOTTINEAU CO: Turtle Mt., *Lunell*, July 23, 1902; Sept. 9, 1902 (RM). CASS CO: Banks of Red River, Fargo, *A. Nelson & A. Nelson* 1018 (RM, MO). DUNN CO: Matt Olson's ranch, Killdear, *Fancy* 235 (TEX). MCHENRY CO: Leeds, *Lunell*, Sept. 10, 1908 (NY). NELSON CO: Stump Lake, *Tufte* 240 (RM). OHIO. BUTLER CO: near Oxford, *Wetmeyer & Waters* 162 (MICH). HAMILTON CO: near Cincinnati, *Lloyd*, May 23, 1888 (MO). LUCAS CO: Reservation, Sylvania, *Wilson* 1482 (WIS). PORTAGE CO: *Webb* 1542 (GH). SCIOTO CO: Shawnee State Forest, Camp Gordon, *Demaree* 10682 (GH, MO). OKLAHOMA. KAY CO: *White* 1898 (NY). SOUTH DAKOTA. FALL RIVER CO: *Visher* 2687 (RM). HARDING CO: 102 (RM). LAWRENCE CO: Piedmont, *Palmer* 37230 (GH). MELLETTE CO: Mellette, *Brenckle* 41-16 (MO). PENNINGTON CO: Spring Creek, *Over* 16208 (RM). SHANNON CO: along wooded River Creek, *Over* 16210 (PH). SPINK CO: near James River e. of Mellette, *Brenckle* 41-16 (GH). WASHABAUGH CO: *Visher* 2280 (NY). TENNESSEE. HARDEMAN CO: slopes near Chickasaw State Park, *Adams* 12684 (TENN). WEST VIRGINIA. HAMPSHIRE CO: Hanging Rock, *Frye* 563 (WVA). WISCONSIN. ADAMS CO: 2 1/2 mi. n.e. of Jhondshy's, *Brown*, July 15, 1948 (WIS). DROWN CO: Treble, *Schuette*, May 19, 1884 (GH). BUFFALO CO: Eagle Bluff, Fountain City, *Fasset & Wilson* 5099 (MICH, WIS). DANE CO: near Monona Village, *Kuhlman* 41 (WIS). DUNN CO: Oakwoods, s. of Elk Mount, *Meyer* 128 (WIS). IOWA CO: sandstone cliff, *Kieckhefer, Lindfors & Thompson*, June 8, 1958 (WIS). JACKSON CO: 2 mi. w. of Hatfield, *Grether* 6726 (WIS). LAFAYETTE CO: 2.5 mi. w. of Gratiot, *Hagens, Melville & Shaughnessy*, Sept. 28, 1956 (WIS). MARQUETTE CO: *Iltis, Trenk & Noamesi* 6354 (WIS). OZAUKEE CO: banks of Milwaukee River, about 3 mi. s. of Fredonia, *Zedler*, June 23, 1963 (WIS). RICHLAND CO: near Sextonville, *Fosberg* 300 & 380 (WIS). ROCK CO: *Croff*, Sept. 23, 1961 (WIS). SAUK CO: Reedsburg,

Hansen 1018 (WIS). ST. CROIX CO: edge of bog n. of Wis. Rt. 64, *H. H. Iltis, F. G. Iltis & G. Noamesi* (WIS). TREMPEALEAU CO: *H. H. Iltis* 6308 (WIS). VERNON CO: Viroqua, *Smith* 7248 (WIS). Bergan Twp., *Hartley* 1029 (WIS). WALWORTH CO: Town of Geneva, *Wadmond* (WIS). WASHBURN CO: Minong, *Fassett* 8601 (WIS). WAUKESHA CO: Musbego, Lake Huron, *Shirler*, July 4, 1928 (WIS); vicinity of Chenequa, w. side of Pine Lake, *Schenke & Niss*, June 18, 1942 (WIS). WYOMING. CROOK CO: Sundance Mt., *R. Nelson* 2139 (MO, RM). CONVERSE CO: Mill Creek, *E. Nelson* 703 (RM). SHERIDAN CO: Dayton, *Tweedy* 2277 (NY).

3. *Smilax pulverulenta* Michx.

Smilax pulverulenta Michaux, Fl. Bor.-Americ. 2:238. 1803.

Type: A. Lourteig of Mus. Nat. Hist. Naturelle, Paris, who examined the Michaux collections, wrote: *"In the folder of *Smilax pulverulenta* Michx. there is no specimen but only the original label. There are no signs of having been any specimen fastened on. Therefore, the specimen of Richards written by himself (who has studied all the plants for Michaux Fl. Bor. Amer.) must be taken as the type specimen". The author examined Richards' specimen in Mus. Nat. Hist. Naturelle, Paris. This specimen is to be considered as the lectotype.

S. herbacea var. *pulverulenta* A. Gray, Manual. 486. 1848.

Shoots up to 2.5 meters high, climbing and branching. Basal leaves small and narrow, larger leaves above 8-16 cm long. On younger plants the basal leaves are the largest and long petiolate. Leaves on branches much smaller, oblong, and with cuspidate tip. Leaves long cordate, margin convex, lower surface shining dark green, pubescent mostly on the veins, tip long acuminate. Inflorescences many, heads globose; peduncles usually equal to or shorter than the subtending leaves. Tepals 3.5-5 mm long, about 1.5 mm broad; anthers 1-1.5 mm long, generally shorter than the filament. Fruit a subglobose berry, 8-10 mm in diameter, with 3-5 seeds. Flowering extends from the third week of April to the first week of June in the north, i.e., about two weeks earlier than *Smilax herbacea* and *S. lasioneuron*.

Distribution is along the Ozark Plateau and Boston Moun-

*Personal correspondence.

tains in Missouri and Arkansas through Tennessee and Kentucky to southern New York, western Pennsylvania, New Jersey, Delaware, Maryland, Virginia, West Virginia, North Carolina and South Carolina. Specimens have been collected from Arkansas, Delaware, Illinois, Indiana, Kansas, Kentucky, Maryland, Minnesota, Missouri, Nebraska, New Jersey, New York, North Carolina, Pennsylvania, Tennessee and Virginia.

The nearest apparent relatives are *Smilax herbacea* and *S. lasioneuron*. Many recognise this species as a variety of *S. herbacea*, but it is markedly distinct from *S. herbacea* by its dark green shiny and pubescent leaf surface and black fruit. *Smilax pulverulenta* flowers about two weeks earlier than *S. herbacea* and *S. lasioneuron*. This behaviour can be considered an isolating mechanism of some importance.

REPRESENTATIVE SPECIMENS: ARKANSAS. INDEPENDENCE CO: Batesville, *Demaree* 17073A (NY). DELAWARE. KENT CO: Woodland Beach, *Schmid, Jr.*, May 11, 1941 (PH). NEW CASTLE CO: Christiana Twp., *Pennell* 1528 (NY). ILLINOIS. JOHNSON CO: Vienna, *Palmer* 14989 (MO). RICHLAND CO: Bird Haven, Olney, *Ridgway*, May 18, 1919 (GH). UNION CO: Pine Hills, *Gleason* 2279 (GH). INDIANA. HARRISON CO: 2 mi. s.e. of Croydon, *Deam* 35561 (PH). HUNTINGTON CO: 3 mi. e. of Andrews, *Henderson* 61-364 (FSU). POSEY CO: near New Harmony, *Cain*, Summer 1932 (TENN). KANSAS. ATCHINSON CO: along Mo. Pac. R.R. in s.e. corner of the County, *Horr* 4460 (GH). KENTUCKY. UNION CO: *Schacklette* 240 (NY). MARYLAND. CECIL CO: moist loamy woods along Great Bohemia Creek, Middleneck, *Long* 37265 (GH). MONTGOMERY CO: Bethesda, *Bartlett* 2180 (FSU). MINNESOTA. DAKOTA CO: *Moore* 15751 (MO). MISSOURI. BARRY CO: 4.5 mi. s.w. of Cape Farr, *Steyermark* 22606 (MO). CLINTON CO: Trimble Wild Life Area, *Howard*, June 21, 1950 (F). DOUGLAS CO: 1 mi. s. of Bryant and Bryant Creek, *Steyermark* 10485 (MO). GENTRY CO: 3 mi. e. of Albany, *Gleason* 9270 (NY, WIS). GREENE CO: *Blankinship*, Sept. 16, 1896 (GH). HOWELL CO: Willow Springs, *Pennell* 11616 (PH). JASPER CO: Webb City, *Palmer* 487 (MO). LACLEDE CO: Lebanon, *Pennell* 11655 (PH). MADISON CO: Mine La Motte, *Greenman* (MO). MARIES CO: s.e. of Vienna, *Steyermark* 73660 (F). MILLER CO: along Little Saline Creek, *Steyermark* 73713 (F). MONITEAU CO: half way up Baker Bluff, *Steyermark* 73342 (F). MORGAN CO: *Steyermark* 72664 (F). NEWTON CO: Sarcoxie, *Palmer* 6277 (F, MO, US). OZARK CO: n. of Gainesville, *Steyermark* 68581 (F). SCOTT CO: bluffs between

Chaffee and Rock View, *Steyermark* 5013 (MO). SHANNON CO: *Bush* 62 (MO). SHELBY CO: *Steyermark* 71704 (F). WASHINGTON CO: *Steyermark* 41186 (F). WEBSTER CO: 1 mi. n. of Rader, *Steyermark* 23774 (MO). NEBRASKA. SEWARD CO: Seward City Park, *Kiener* 17091 (F). NEW JERSEY. BURLINGTON CO: 1 mi. w. of south Branch of Raccoon Creek, Vince town, *Long* 48322 (GH). GLOUCESTER CO: moist wooded slope 1.5-2 mi. w. of Mullica Hill, south branch of Raccoon Creek, *Long* (GH), MERCER CO: moist rocky wooded slope, Baldpate Mt. facing Titusville, *Long* 30394 (GH). SALEM CO: Riddleton, *Beales & Bassett*, Aug. 31, 1924 (RM). NEW YORK. BRONX CO: south of Van Cortland Park, *Pennell* 7040 (PH). ORANGE CO: Black Rock Forest, *Raup* 7523 (MICH). RICHMOND CO: Princess Bay, Staten Island, *Mrs. L. M. Parker*, May 25, 1889 (GH). NORTH CAROLINA. ALAMANCE CO: 3 mi. s. of Swepsonville, *Radford* 10663 (NCU). AVERY CO: 4 mi. s. s.e. of Banners Elk on N.C. Rt. 184, *Ahles* with *Duke* 47473 (NCU). BUNCOMBE CO: Ashville, May 11, 1924 (GH). CLAY CO: 8 mi. e. of Buck Creek on U.S. Rt. 64 about 8 mi. s.e. of Clay Macon County line, *Ahles* with *Radford* 13555 (NCU). GASTON CO: 1 mi. s. of Mtn. View, near Crowders Mt., *Ahles* with *Leisner* 15051 (NCU). IREDELL CO: 4 mi. e. of Harmony on branch of Hunting Creek, *Ahles* with *Duke* 45209 (NCU). JOHNSTON CO: 1.6 mi. n. n.e. of Clayton, *Radford* 21717 (NCU). LEE CO: w. side of Fall Creek, 6 mi. n.e. of Broadway, *Stewart* 387 (NCU). ORANGE CO: Seven Mile Creek, just s. of Efland, *Ahles* with *Williamson* 53278 (NCU). PERSON CO: .5 mi. n. of Surl, *Bell* 12363 (NCU). ROCKINGHAM CO: deciduous forest near N.C. Rt. 14, s. of Leaksville, *Radford* 10799 (NCU). ROWAN CO: 2.6 mi. n.w. of Craven, 5.3 mi. n.e. of Granite Quarry, *Horton* 1104, (NCU). SWAIN CO: .3 mi. s. and 1.9 mi. e. of Alarka, *Bell* 3254 (NCU). YANCEY CO: 3.3 mi. n. of Swiss, *Ahles* with *Duke* 42718 (NCU). PENNSYLVANIA. BERKS CO: *Wilkens* 7117 (MO). DELAWARE CO: Wawa, *Pennell* 14495 (NY). FRANKLIN CO: Mercersburg, *Porter* May 28, 1850 (PH). LANCASTER CO: bank of Little Connestoga, Lancaster, *Heller*, May 18, 1889 (GH). NORTHAMPTON CO: Easton, *Green*, Aug. 31, 1859 (GH). PHILADELPHIA CO: Philadelphia, near Fairmont Park, *Parker*, May 24, 1862 (NY). YORK CO: far below McCall's Ferry, *Crawford*, July 3, 1904 (PH). SOUTH CAROLINA. DARLINGTON CO: edge of Black Creek near Darlington Country Club, *B. E. Smith* 221 (NCU). YORK CO: Sugar Creek on S.C. Rt. 160, e. of Fort Mill, *Ahles* with *Haesloop* 27209 (NCU). TENNESSEE. ANDERSON CO: Keith Farm Bluffs, Morris, *Varnell*, May 24, 1937 (TENN). HARDEMAN CO: roadside slope near Lowton, *Sharp, Fairchild, E. Clebsch & A. Clebsch* 9330 (TENN). KNOX CO: Knoxville, May 1898 (NY). LOUDON CO: Quarry Bluff near Lenoir City, *Cain & Sharp* 4508 (TENN). SHELBY CO: slope of bluff in Shelby Forest Park, *Adams* 10447 (TENN). UNION CO: Rhodelia Unit, Norris Lake Forest, *Morrison*, June 16, '37 (TENN). TIPTON CO: slope near Anglican Spring near

Richardson, *Sharp, Felix & Adams* 12158 (TENN). VIRGINIA. CULPEPPER CO: Waterloo, *Meredith*, May 24, 1922 (PH). FREDERICK CO: Belle Grove, *Hunnewell* 17850 (GH). JAMES CITY CO: Matoak Park, *Baldwin, Jr.*, (GH). PRINCESS ANN CO: rich woods, Great Neck, *Fernald & Griscom* 4357 (GH). SMYTHE CO: Marion, *E. G. Britton & Vail*, May 22, 1892 (NY). SOUTHAMPTON CO: rich sandy and loamy woods along Three Creeks, n.w. of Carey Bridge, *Fernald & Long* 10210 (GH). SURRY CO: rich calcareous wooded ravines along James River, Clarement, *Fernald & Long* 13589 (GH). SUSSEX CO: rich deciduous woods along Nottoway River, s.w. of Homeville, *Fernald & Long* 10205 (GH). 6 mi. n.w. of Jarratt, *Fernald & Long* 11302 (GH, MO). WEST VIRGINIA. FAYETTE CO: river banks below depot, *Nuttall*, July 16, 1894 (WVA).

4. *Smilax pseudo-china* L.

Smilax pseudo-china L. Sp. Pl. 1031. 1753.
Type: Linnacean Herbarium, London, marked by Linneaus, "K. pseudo-china". This specimen was collected by Kalm in New Jersey or Delaware.

S. inermis Walt. Fl. Carol. 244. 1788.
According to Pennell "Type presumably from Berkeley County, South Carolina". Not verified.

S. tamnifolia Michx. Fl. Bor.-Am. 2:238. 1803.
Type: Michaux herbarium, in Mus. Nat. Hist. Natu., Paris. An isotype, Dr. Richard's specimen in Mus. Nat. Hist. Natu., Paris, labelled Smilax tamnifolia Michaux examined. A. Lourteig, who compared this specimen with the type, agrees it looks exactly like the type specimen.

Coprosmanthus tamnifolius (Michx.) Kunth, Enum. Pl. 5: 267. 1850.

Nemexia tamnifolia (Michx.) Small, Fl. S.E. U.S. 281. 1903.

S. leptanthera Pennell, Bull. Torr. Bot. Cl. 43, 412, 1916.
Type:! S. M. Tracy Coll. No. 9257 (NY). Collected from Warm Springs, Georgia, on May 22, 1905. Apparently an ecological variant with slightly larger and thinner leaves.

Smilax pseudo-china was included with *S. lanceolata* by Linnaeus in a section with unarmed terete stems. Pennell

(1916) considered the type specimen of this Linnean species as a duplicate of *S. herbacea* L. and accepted *S. tamnifolia* Michx. as the legitimate name of the species. I am in complete agreement with M. L. Fernald* (1944) who made a thorough investigation of the whole nomenclatural problem and, after a careful examination of the type specimens, came to the conclusion that *S. pseudo-china* L. is the same as *S. tamnifolia* Michx. and because of priority *S. pseudo-china* is to be considered as the legitimate name.

Shoots up to 2 meters high, climbing, and occasionally branching, basal leaves on older stems may be small and narrow, tendrils developing from most leaf bases. Leaves many, 5-12 cm long, thin, glabrous and glaucous beneath, larger leaves hastate, with concave margin, truncate to subcordate at base, apex rounded and cuspidate; three veins reaching the tip; peduncles solitary or in threes in the axils of leaves, often equal to the subtending leaf, if peduncles are three in number from the same axil the middle one will be the longest and with more flowers, with 10-30 flowers in a loose globose head. Tepals oblong or ovate 1.5-2.5 mm long, about 1 mm broad; anthers 0.5-1 mm long, equal to or slightly longer than the filament; style elongate, ligulate; fruit a subglobose berry, glaucous, 4-6 mm in diameter, black, 1-3 seeded. Flowering begins in the first week of May in the Carolinas and reaches the peak in the second week, progressively later to the north, up to the second week of July.

Smilax pseudo-china occupies the outer coastal plain from New Jersey and Delaware to South Carolina and Georgia. Fernald (1944) suggested the presence of a gap in distribution between South Carolina and southern Virginia, as frequently known in other species. But *S. pseudo-china* has been collected from this area. Specimens have been collected from Delaware, District of Columbia, Georgia, Maryland, New Jersey, North Carolina, Pennsylvania, South Carolina and Virginia.

Its closest relative apparently is *Smilax herbacea* with

*Fernald *Rhodora* **46**: 542; 32-60.

smooth, glaucous leaves. *Smilax pseudo-china* with its chromosome number $2n = 30$ is likely an aneuploid.

REPRESENTATIVE SPECIMENS. DELAWARE. NEW CASTLE CO: South Wilson, *Pennell* 13255 (NY). DISTRICT OF COLUMBIA. WASHINGTON CO: Kensington Swamp, *Peters*, Aug. 6, 1899 (MICH). GEORGIA. MCDUFFEE CO: *Bretlett* 1130 (MICH). MERIWETHER CO: Warm Springs, *Tracy* 9529 (TEX). UPSON CO: s. of Elkins Creek, *Duncan* 6553 (GA). MARYLAND. PRINCE GEORGES CO: near Clinton, *Holm*, June 12, 1925 (LCU). NEW JERSEY. BURLINGTON CO: N.J. Brown's Mills, *Pennell* 13249 (NY). CAPE MAY CO: *Pennell* 2232 (US). MONMOUTH CO: *Alsbury*, July 4, 1910 (MICH). NORTH CAROLINA. NURNSWICK CO: west of Wilmington, *Leeds* 1311 (PH). GASTON CO: base of Spencer Mt., 1 mi. s. of town of Spencer Mt., *Ahles* with *Leisner* 15000 (GH). GATES CO: 2 mi. n.e. of Hartford, Gates County line, *Ahles* with *Duke* 48403 (NCU). HOKE CO: 3.2 mi. s.w. of Rockfish, *Ahles* with *Neuber* 25162 (NCU). MARTIN CO: 0.6 mi. n.w. of Gold Point, *Radford* 41910 (GH, NCU). MOORE CO: Drowning Creek, on U. S. Rt. 1, *Gupton* 1602 (NCU). ONSLOW CO: *Ashe*, Sept. 1904 (NCU). ROBESON CO: 4.5 mi. out of Allenton and 0.3 mi. s. s.w. on dirt road, *Ahles* 29037 (NCU). PENNSYLVANIA. DELAWARE CO: Tinicum, *Porter*, Sept. 12, 1863 (GH, NY). SOUTH CAROLINA. BERKELY CO: Bog on Savannah, 1 mi. w. of Chicora, *Godfrey* & *Tryon, Jr.* 868 (NY, US). CHARLESTON CO: 14 mi. s. of Charleston, *Moldenke* 1196A (NY). CHESTERFIELD CO: 2 1/2 mi. n. of Patrick, near U. S. Rt. 1, *Radford* 12449 (NCU). CLARENDON CO: Pine Barrens, 2 mi. n. of Manning, *Stone* 245 (PH). COLLETON CO: 0.7 mi. s.e. of Hiotts, 1.5 mi. n.w. of Sidney on Co: 45, *Ahles* with *Bell* 12216 (NCU). HAMPTON CO: *Bell* 2549 (NCU). HORRY CO: 2 mi. s. of Loris, *Bell* 7766 (NCU). JASPER CO: 1 m. s. of Hampton ,on S.C. Rt. 128 *Bell* (NCU). KERSHAW CO: 4 mi. e. s.e. of Westville, *Radford* 23682 (NCU). MARION CO: 1.3 mi. n. of Gresham, on S.C. Rt. 9, *Bell*, July 2, 1958 (NCU). ORANGEBURG CO: 1.9 mi. s.e. of jct. Rts. U.S. 15 & 176 on Rt. 176, n.w. of Holly Hill, *Ahles* with *Haesloop*, July 18, 1957 (NCU). SALUDA CO: 1.4 mi. s. of Ridge Spring, *Radford* 23097 (NCU). VIRGINIA. CHESTERFIELD CO: south of Manchester, *Wherry* & *Pennell* 14467 (PH). DINWIDDIE CO: "Reams Bog", s. of Burgess, *Fernald* & *Long* 9029 (GH). GREENVILLE CO: Mill Swamp, s. of Emporia, *Fernald* & *Long* 10587 (GH). JAMES CITY CO: 5 mi. w. of Williamsburg, *Grimes* 3806 (NY). NANSEMOND CO: Dismal Swamp, 9 mi. n. of Lake Drummond, *Ahles* with *Coker* 58336 (NCU). NORFOLK CO: Great Dismal Swamp, n. of Yadkin, *Fernald* & *Long* 12301 (GH). NORTHAMPTON CO: s. of Kendall Grove, *Fernald, Long* & *Fogg, Jr.*, 5271 (GH). PRINCE GEORGE CO: about 3 mi. s.e. of Petersburg, at head of Poo Run, *Fernald, Long* & *Smart* 5722 (GH). SOUTHAMPTON CO: Franklin, *Heller, Jr.*, 925 (GH); near Blackwater River, Cobb's Wharf, *Fernald* & *Long* 10206, 1939 (GH). SUSSEX CO: n. of Wakefield, *Fernald* & *Long* 7383 (GH).

5. **Smilax illinoensis** sp. nov.

Typus: Dane Co., Wisconsin; *John Schaars*, Oakwoods (T8N; R9E; Sect. 32), May 15, 1958 (WIS).

Caulis 0.5-1.0 m longus, erectus, ad extremum cirris paucis, rare divisus. Folia multa, bracteolata, ab subtilis, inferiora majora, superiora minora. Petioli longi laminis leviter anguste ovatis, inferne pubescentibus, base ovato-truncata vel leviter cordata, margine convexa, extreme acuto-acuminato. Peduncula 3-10, inferiora longa, bracteis axillaria, floribus 10-50 in cacuminibus semiglobosis, tepalia 3.5-4.5 mm longa, 1.5-2.0 mm lata. Antherae 1.2-5 mm longae, filamento breviores. Baccae globosae, semina 3-5. Invenitur multum apud regionem "Great Lakes", Americae Septentrionalis.

Shoots 0.5-1.0 meter high, erect with few short tendrils, mostly at the top, rarely branching; usually transition from bract to leaf is abrupt. Leaves many, thin at anthesis, larger leaves below and progressively smaller above, petioles long, blades narrowly ovate, pubescent beneath, margin convex, base ovate to truncate, and tip acute to acuminate. Peduncles 5-10, lower ones long and axillary to the bracts, with 10-50 flowers in a semiglobose head at top (Fig. 25). Tepals 3.5-4.5 mm long, 1.5-2.0 mm broad. Anthers 1.2-1.5 mm long, usually shorter than filaments. Fruit a globose berry, 3-5 seeded. Flowering begins in the first week of May and lasts to the second week of June.

Distribution is mostly in the Great Lakes Region, in thickets along the roadsides. Specimens have been collected from Arkansas, Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, Ohio and Wisconsin and from Canada close to the Great Lakes.

This species is close to *Smilax lasioneuron* and *S. ecirrhata* and is often identified as either of these species. It differs from *S. lasioneuron* by its short erect bushy nature, long petiole and thin leaves with acute to truncate base. In general, it is taller than *S. ecirrhata* and with its conical nature with many long petiolate leaves and ovate to truncate leaf bases and many short tendrils, it is distinct from

S. ecirrhata. However, it resembles *S. ecirrhata*, being erect, and the lower peduncles developing from bract axils. It is possible that this species might have resulted from past hybridization with or without back crossing.

REPRESENTATIVE SPECIMENS: ILLINOIS. CHAMPAIGN CO: Urbana, *Gates* 2335 (WIS). DU PAGE CO: Naperville, *Powell*, May 21, 1898 (WIS). KANE CO: 7 mi. w. of Aurora, *Erlanson*, Aug. 1923 (MICH). RICHLAND CO: Larchmound, Olney, *Ridgway* 723 (GH). SANGAMON CO: *Lodewyks* 362 (MO). STARK CO: near Wady Petra, *Chase*, May 26, 1900 (F). ST. CLAIR CO: *Eggert*, May 8, 1892 (MO). INDIANA. HOWARD CO: 3 mi. n.w. of Kokomo, *M. Ek*, May 5, 1942 (GH). TIPPECANOE CO: 4 mi. n. of Lafayette, *Deam* 54807 (MO). SHELBY CO: 4 mi. s.e. of Shelbyville, *Friser* 17695 (GH). WILLS CO: 1/4 mi. e. of Bluffton, *Deam*, July 2, 1905 (MO). IOWA. BOONE CO: *Swailes*, May 20, 1952 (PH). DUBUQUE CO: 2 mi. n.w. of Luxemburg *Grether* 8159 (WIS). JASPER CO: *Jones*, May 11-26, (GH). JOHNSON CO: *T. J. Fitzpatric & M. F. L. Fitzpatrick*, May 13, 1900 (US). MICHIGAN. GRATIOT CO: *A. Davis*, May 15, '95, June 12, '95 (MICH). INGHAM CO: East Lansing, *Stewer* May 25, 1938 (MICH). KENT CO: Grand Rapids, *Bailey*, June 11, 1892 (MICH). LAPEER CO: Flint River, *Voss* 8236 (MICH). MARQUETTE CO: west bank of the Escamba, *Harrison*, June 8, 1908, MIDLAND CO: along Salt River, 4 mi. s. of Colman, *Dreisbach* 6702 (MICH). ONTOMONGAN CO: Porcupine Mt., *Richards* 3076 (MICH). SHIAVASSEE CO: Owasso, *Hicks*, May 18, 1889 (MICH, US). SAGINAW CO: *Carr, Jr.*, May 30, 1956 (MICH). WASHTENAW CO: Ann Arbor, *La Rue*, May 18, 1915 (MICH). *Grassel* 5272a (MICH). WAYNE CO: Belle Isles, Detrioit, *Farwell*, May 23, '95 (MICH). MINNESOTA. RAMSEY CO: *Sheldon*, May 1891 (RM). RICO CO: Northfield, *Goldsmith* 1912 (NY). MISSOURI. JEFFERSON CO: near Barnhart, *Steyermark* 1066 (MO). PIKE CO: Sandy Creek, 4 1/2 mi. s.e. of Cyrene, *Steyermark* 28611 (F). SCHUYLER CO: *Steyermark* 69915 (F). WISCONSIN. ASHLAND CO: Ashland, White River bottom, *Robb* 121 (WIS). BROWN CO: Loin Wood, *J. H. Smith* 12. 1-114 (F). CALUMET CO: 1 mi. s. of Brillion on Rt. 114, *Strandberg* 104 (WIS). CLARK CO: s.e. of Stanley, *Schmidt*, June 4, 1933 (WIS). COLUMBIA CO: n. of Fall River on County trunk, *Oelke & H. Edwards* (WIS). DANE CO: *Schaars*, May 15, 1958 (WIS). FOND DU LAC CO: Taychudah, *Fassett, Cunningham & Erdman* 15251 (WIS). GREEN CO: 3 mi. n. of Albany, *Hammerstrom*, May 28, 1928 (WIS). *Wadmond*, Sept. 15, 1929 (WIS). IOWA CO: R. Hansen Farm, *Swan* 39 (WIS). JEFFERSON CO: Lake Mills, *Fassett* 8092 (WIS). JUNEAU CO: 4 mi. e. of Necedah, *Fernhalz*, May 14, 1930 (WIS). KEWAUNEE CO: 1 mi. w. of Dyckesville, *Iltis, Schlising & Johnson* 17384 (WIS). LAFAYETTE CO: along Pectonica River, 5 mi. n. of Belmont, *Stichney*, May 17, 1959 (WIS). LANGLADE CO: woods on Hwy. 64, across from Black Brook, *Owen* 140 (WIS). MANITOWOC

CO: jct. Rts. 149 & M. Spring Valley, *Tryon, Jr.* 3523 (WIS). POLK CO: St. Croix Falls, *Fassett* 15555 (WIS). RICHLAND CO: Kepter Ridge, *Heinstein,* May 15, 1962 (WIS). ROCK CO: Janesville, *Mead & Blunt,* May 29, 1930 (WIS). SAUK CO: Reedsburg, *Fassett & Curtis* 20054 (WIS). SHEBOYGAN CO: Sheboygan, *Goessl,* June 6, 1914 (WIS). VERNON CO: Viroqua, *Hanson* 240 (WIS). WALWORTH CO: along CMS & P and Pac. R.R. right-of-way, "Springfield Hill", *Wadmond,* Sept. 20, 1929 (WIS). WASHINGTON CO: Hartford, *Quandt,* June 1, 1929 (WIS). WAUKESHA CO: west side of Lake Nehmabin, *Ugent,* May 19, 1957 (WIS).

6. *Smilax ecirrhata* (Englemann ex Kunth) S. Watson

Coprosmanthus herbaceus var. *ecirratus* Engelm. ex Kunth Enum. Pl. 266. 1850.
Type: Engelman in Herb. reg. Berol probably destroyed in World War II. Photograph of Engelmann specimen in the Boissier herbarium (G) designated 'Type' examined. This specimen with its long petiolate narrow leaves is atypical of the species. Another specimen from Engelmann's collection, typical of *S. ecirrhata,* labelled "*Smilax herbacea,* grassy woods east of Bellesville, Ill., May 1835" and later annotated by him as "*Smilax acirrha* nov. Mai 1835" is found in herb. Missouri Bot. Gard., St. Louis. This specimen should be considered as the lectotype of the species. Even though the epithet *ecirrhata* was first applied by Engelmann, it was first validly published by Kunth in 1850.

Smilax herbacea var. *ecirrhata* (Engelm. ex Kunth) A. DC Monogr. Phan. I: 52. 1878.

Smilax ecirrhata (Engelmann ex Kunth) S. Watson. A. Gray's Man. ed. 6, 520. 1890.

C. ecirrhatus (Engelm. ex Kunth) Chapman, Fl. S. U. ed. 3, 504. 1897.

Nemexia ecirrhata (Engelm. ex Kunth) Small, Fl. S.E. U.S. 280. 1903.

Shoots 3-8 dm high, erect, with few or no tendrils, and with long lower internodes. The lower third or one half of the stem with bladeless bracts; leaves equally distributed on the upper part of the stem, progressively smaller up-

ward, petioles definitely shorter than the blade, blade broad ovate, subrotund or cordate, pubescent beneath (not prominently on the veins), thin, base truncate to cordate, margin convex, tip round and pointed to acuminate: Peduncles usually 1-3, the lower ones from bract axils below foliar leaves, umbels few, flowered and hemi-spherical. Tepals 3.5-4 mm long, about 1.5 mm broad, anthers 1.2-1.5 mm long subequal to filaments. Fruit a globose berry, purple black and 3-5 seeded. Flowering begins in the first week of May and extends to the second week of June.

Distribution is mostly in roadside thickets in the Mid-central Plains and the Great Lakes Region. Specimens have been collected from Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Ohio, Oklahoma, Tennessee, and Wisconsin.

Its closest relatives apparently are *Smilax huberi* and *S. biltmoreana*. Both are shorter and with fewer leaves approximate at tip and they differ from *S. ecirrhata* mainly in their leaf shape. Leaves of *S. biltmoreana* are nonpubescent.

REPRESENTATIVE SPECIMENS. ILLINOIS. CHAMPAIGN CO: Urbana, *Gates*, May 31, 1907 (GH). 2329 (MICH). Brownfield Woods, Somer, *Pease* 11, 895 (GH). COOK CO: Stony Island, Chicgao, *Greenman* 3643 (GH). DU PAGE CO: *near* Roselle, *Chase* 9418 (F). GALLATIN CO: *Palmer* 15326 (MO). KANE CO: *Steyermark* 68342 (F). LAKE CO: 5 mi. n. of Barrington, *Steyermark* 63526 (F). LA SALLE CO: Starved Rock State Park, *Lansing, Jr.*, 3859 (F). MARSHALL CO: west fork of Senachequine Creek near Lawn Ridge, *Chase*, May 19, 1907 (MICH). PEORIA CO: 1 1/2 mi. s.e. of Princeville, *Chase* 1678 (NY). RICHLAND CO: Larchmound, Olney, *Ridgway* 722 (GH). ST. CLAIR CO: *Eggert*, May 8, 1892 (MO). INDIANA. PORTER CO: 5 mi. s.e. of Michigan City, Notre Dame, *Nieuwland*, May 15, 1910 (US). IOWA. FAYETTE CO: *Fink* 395 (US). HARRLSON CO: *Burgers* (NY). IOWA CO: rich woods n. of Middle Amana, *Easterly* 175 (WVA). JOHNSON CO: MacBridge State Park, *Kennedy & Kluss* 40 (NCU); Big Grove Twp., *Davis & Pfeifer*, May 20, 1956 (NCU). SCOTT CO: Wapsi Bottoms, St. Ambrose College 2137a (LCU). SIOUX CO: Oak Grove State Park, *Carter* 120 (NCU). KENTUCKY. KNOX CO: 6 mi. n. of Knoxville on U. S. Rt. 25, *Hobb* 105 (NCU). NELSON CO: *Sr. Agnes* 1391 (LCU). MICHIGAN. BARRY CO: *Haugen* 236 (MICH). BRANCH CO: Butler Twp., *Voss* 3703 (MICH). HOUGHTON CO: near mouth of Sturgeon River, *Richards*

1267 (MICH). JACKSON CO: *S. H. & R. D. Camp*, May 20, 1894 (WIS); May 20, 1897 (F). LAPEER CO: n.e. side of Big Fish Lake, *Voss* 7287 (MICH). MACOMB CO: s. of Utica, *Billington*, June 10, 1917(MICH). MENOMINEE CO: City of Menominee, *Grassl* 2835 (MICH). ST. CLAIR CO: near Port Huron, *Dodge*, Aug. 21, '92 (MICH). TUSCOLA CO: 8.5 mi. e. of Cairo, *Voss* 7346 (MICH). WASHTENAW CO: Cascade Glen, West Ann Arbor, *Erlanson* 117 (MICH). New Comb Tract Forest, *Fordal* 1636 (NCU). WAYNE CO: Detroit, *Austin*, May 1863 (GH); Wayne, *Farwell* 9150 (MICH). MINNESOTA. RAMSEY CO: *Sr. St. Lawrence* 57, (LCU). MISSOURI. CARROLL CO: 1/2-1 mi. n. of Mandeville, *Steyermark*, June 10, 1952, (F). CHRISTIAN CO: *Steyermark* 23165 (MO). CLARK CO: along Des Moines River 1/2-1 1/2 mi. n.w. of Athens, *Steyermark* 28694 (GH). HARRISON CO: *Steyermark* 10962 (MO). JEFFERSON CO: *Eggert*, Aug. 24, 1892 (MO). JOHNSON CO: 3 1/2 mi. n. of Holdon, *Steyermark* 67860 (F). LEWIS CO: *Steyermark* 25635 (MO). LINN CO: 6 mi. s.w. of New Boston, *Steyermark* 40480 (GH). MACON CO: *Bush* 7632 (GH, NY). MERCER CO: *Steyermark* 7850 (MO). MILLER CO: *Steyermark* 13078 (MO). MONROE CO: *Steyermark* 66542 (F). MORGAN CO: *Bush* 13743 (MO). MONTGOMERY CO: *Steyermark* 65353 (F). OSAGE CO: e. of Durcoe, *Steyermark* 10730 (MO). PETTIS CO: 2 1/2 mi. s. of Sedalai, *Steyermark* 67988 (F, MO). PIKE CO: Curryville, *Steyermark* 74358 (F). PUTNAM CO: *Steyermark* 73574 (F). SCHUYLER CO: east side of Charton River, e. of Livonia, *Palmer & Steyermark* 41058 (A). SCOTLAND CO: Iron Mt. area, *Steyermark* 74447 (F). OHIO. ERIE CO: Perkins, *Moseby*, Sept. 12, '97 (GH). LUCAS CO: *James C. Myers*, Aug. 12, 1940 (WVA). OKLAHOMA. ADAIR CO: 7 mi. s.w. of Stillwell, *Moore* 55-84 (WIS). TENNESSEE. KNOX CO: Knoxville, w. of T. Farm, *Iltis* 1700 (WIS). WISCONSIN. BROWN CO: near Atkinson, *Schuett*, May 6, 1890 (NY). DANE CO: Madison, *Dauffman*, May 27, 1902 (MICH). GREEN CO: Co. K, Twin Grove Rd., *Fell* 57-1463 (WIS). JEFFERSON CO: Wollein's Woods, Milford Twp., *Allen & Wright*, June 3, 1938 (WIS). PIERCE CO: Diamond Bluff, *Wadmond, Fassett, Sperry & Reeve* 18193 (WIS). SAUK CO: Parfrey's Glen, Merrimac Twp., *Fassett* 2930 (WIS); *Erickson & Johnson*, May 27, 1960 (WIS). TAYLOR CO: Diamond Lake, Roosevelt Twp., *Piehl* 321 (WIS). VERNON CO: Koeth's Wood, *Hartley, Thorne & Hartley* 251 (WIS).

7. *Smilax hugeri* (Small) J.B.Norton ex Pennell

Nemexia hugeri Small, Fl. S.E.U.S. 280. 1903.

Type! N. Y. Bot. Garden. Collected on and about Stone Mountain (100-1500 feet), De Kalb County, Georgia by J. K. Small, May 1-18, 1895. Stem "6-12 inches high, leaves uncial" elliptic leaves, acute at each end, from Alabama.

Smilax hugeri (Small) J. B. Norton ex Pennell in Bull. Torr. Bot. Cl. 43: 420. 1916.

Smilax ecirrhata var. *hugeri* (Small) Ahles, Jour. Elisha Mitch. Sci. Soc. 8: 172. 1964.

Shoots 2-5 dm tall, erect, tendrils usually none, or very few and rudimentary. Leaves few, approximately at top or equally distributed, more or less equal in size, oblong oval, 8-12 cm long, pubescent beneath, base ovate to slightly cordate, broadly rounded and obtuse or abruptly pointed at the apex. Peduncles 1-3, the lower ones mostly from bract axils, umbels few flowered. Tepals oblong, 3-3.5 mm long, 1.25-1.5 mm broad. Anthers 1-1.5 mm long, shorter than filaments. Fruit a globose berry 8-10 mm in diameter. Seeds 2-3. Flowering begins in the first week of April and lasts to the second week in May.

Distribution is restricted to the southeastern part of the United States. Specimens have been collected from Alabama, Florida, Georgia, North Carolina, South Carolina, and Tennessee. Specimens from Tennessee are not so sharply defined as elsewhere and often are taxonomically puzzling. This is taken as possible evidence of the divergence that has occurred in the *Smilax ecirrhata* complex in this region.

The closest relatives, apparently, of this species are *Smilax biltmoreana* and *S. ecirrhata*. However, it differs from both mainly in the morphology of the leaf.

REPRESENTATIVE SPECIMENS: ALABAMA. JACKSON CO: Bryant, *L. V. Porter*, April 29, 1939 (GH). AUTANGA CO: *Harper* 3169 (MO). LEE CO: Auburn, *Earl & Baker*, Sept. 8, 1897 (NY). FLORIDA. GADSDEN CO: Gadsden, *Chapman*, 1835 (NY). JACKSON CO: Marianna Caverns State Park, *Mitchell* 982 (FSU). LEON CO: mixed forest, *Karz*, Aug. 13, 1942 (FLAS). GEORGIA. CLARKE CO: 1/2 mi. s. of Hull, *F. Harper* 1560, May 20, 1940 (PH). CLAY CO: along Cemochechobee Creek, n. of Forest Gaines, *Thorne* 3462 (GH). DADE CO: 2.8 mi. e. of Rising Fawn, road to Lookout Mt., *McVaugh* 5591 (FSU). EFFINGHAM CO: 4 mi. n.e. of Stillwell, *Hardin & Duncan* 15151 (GA). MARION CO: n. of Buena Vista, *R. M. Harper*, July 10, 1902 (MO). RICHMOND CO: *Cuthbert*, Sept. 15, 1899; Fruit, May 5, 1900; Fl. April 25, 1903 (FLAS). NORTH CAROLINA. ANSON CO: 3 mi. s. of Wadesboro, *Radford* 43596 (NCU). MACON CO: 1/2 mi. s.w. Ellijay, *Radford*, June 22, 1946 (NCU). SOUTH CAROLINA. AIKEN CO: 1.3 mi. w. of jct. U. S. Rt. 176 & S. C. Rt. 254 on U. S. Rt. 176, *Ahles*

55138 (NCU). ALLENDALE CO: 2 mi. s.w. of Barton, on Co. 68, *Bell* 10660 (FSU, GA, NCU). BAMBERG CO: 2 mi. e. n.e. of jct. Co. 18 & S. C. Rt. 362 on Co. 18, *Ahles* with *Haesloop* 22235 (GH, NCU). BARNWELL CO: *C. L. Porter*, June 10, 1956 (NCU). CALHOUN CO: Swamp Creek on S. C. Rt. 261, e. n.e. of Cameron, *Ahles* with *Haesloop* 21821 (NCU). CHESTER CO: near Catawba River at Great Falls, *Radford* 43501 (NCU). CLARENDON CO: 6.5 mi. south of Jordan, *Radford* 24634 (NCU). COLLETON CO: woods near swamp on U. S. Rt. 21, 2 mi. n.w. of jct. U. S. Rt. 17A, *Bell* 4611 (NCU). DARLINGTON CO: Hartsville, *Norton* 357 (US). DORCHESTER CO: Little Creek on Co: 130, s.w. of Reevesville, *Ahles* with *Haesloop* 26238 (NCU). GEORGETOWN CO: Brookgreen, *Tarbox*, May 17, 1943 (NCU). KERSHAW CO: near S. C. Rt. 97, 8 mi. w. of Camden, *Radford*, 20882 (NCU). LANCESTER CO: s. s.w. of Lancaster, *Ahles* 23075 (NCU). LEXINGTON CO: vicinity of Batesburg, *McGregor* 501 (US). MC CORMICK CO: near Stevens Creek, 2 mi. n.e. of Clarks Hill, *Radford* 43530 (NCU). ORANGEBURG CO: 3.7 mi. s.w. of Neeses on S. C. Rt. 4, *Ahles* with *Haesloop* 25305 (NCU). RICHLAND CO: Columbia (Charleston), *Smyth*, June 1891 (NCU). SUMTER CO: 4 1/2 mi. w. of Pine Wood near Milford, *Radford* 21013 (NCU). WILLIAMSBURG CO: 5 mi. s. of Gourdin, *Radford* 21390 (NCU). TENNESSEE. ANDERSON CO: Cove Creek Dam road via Cross road, *Underwood* 283 (TENN). BLOUNT CO: limestone bluff along highway to Park near Walland, *Sharp* 28147 (TENN). CLAIBORNE CO: near Harrowgate, moist shaded slope along Powell River above Bridge, *Sharp & Creer* 26840 (TENN). COFFEE CO: moist shaded creek bottom, Rutledge Falls near Tallaloma, *Sharp, A. Clebsch & E. Clebsch* 4704 (TENN). FRANKLIN CO: rocky slope near quarry along Wewanee Winchester road, *Shanks* 1871 (TENN). GRUNDY CO: wooded limestone slope of Cumberland H. Mont Eagle, *Svenson* 7652 (TENN). KNOX CO: Knoxville, *Ruth* 441 (GH); on hillside in woods, Cherokee, *Hesler* 368 (TENN); hillside sloping toward "Sink Holegate" on U. T. Farm, Knoxville, 1 mi. from Knoxville, *Iltis*, May 5., 1943 (TENN). LOUDON CO: Lenoir City, woods 2 mi. s., *Cain & Sharp* 4484 (TENN). MORGAN CO: woods above Petros, *Underwood* 32687 (TENN). POLK CO: moist slope near Hiwasee River, w. of Reliance, *Mr. & Mrs. Sharp, Jones, Varner & Ramsey* 30986 (TENN). ROANE CO: slope along Creek, 4 mi. out Rt. 61 from Harriman toward Oliver Spring, *Sharp, Ellis & Adams* (TENN). SCOTT CO: growing on steep slope between Norma and Montgomery, *Sharp* 25678 (TENN). UNION CO: Walden's Ridge, Effie, Island F, Norris Lake, *Mrs. Kelley*, April 29, 1935 (TENN). VAN BUREN-BLEDSOE CO: Cumberland Plateau, *Iltis* 3196 (TENN).

8. *Smilax biltmoreana* (Small) J. B. Norton ex Pennell

Nemexia biltmoreana Small, Fl. S.E. U.S. 281. 1903.

Type! Biltmore herbarium No. 906b, now in New York

Botanical Garden. Biltmore, N. C., May 4, 1897, J. K. Small.

Smilax biltmoreana (Small) J. B. Norton ex Pennell, Bull. Torr. Bot. Cl. **43**: 413. 1916.

S. ecirrhata var. *biltmoreana* (Small) Ahles, Jour. Elisha Mitch. Sci. Soc. **80**: 172. 1964.

Shoots 2-6 dm high, erect, without tendrils. Leaves few approximate at tip, ovate, 6-12 cm long, wholly glabrous and glaucous beneath, thick even at anthesis, cordate at base, tip acute to acuminate. Peduncles 1 to few, lowest ones mostly from the axil of the lowest leaf or from a bract axil. Flowers few. Tepals of the staminate flowers ovate to oblong, 2.5-3.5 mm long, 1.25-1.5 mm broad. Anthers about 1.5 mm long, longer than filaments. Fruit a globose berry, with 2-3 seeds. Flowering is mostly in the third and fourth weeks of May.

Distribution is restricted to the Mountain Region of southeastern United States. Specimens have been collected from Alabama, western Florida, Georgia, North Carolina and western South Carolina.

Apparently, its nearest relatives are *Smilax hugeri* and *S. ecirrhata*. It differs from both by the absence of pubescence and in the leaf shape.

REPRESENTATIVE SPECIMENS: ALABAMA. ESCAMBIA CO: hardwood slashpine forest, Ept. Forest s. of Brewton and e. of Highway 93, *Ford* 5209 (FLAS). FLORIDA. JACKSON CO: Marianna Cavern State Park, *Mitchell* 972 (FSU). GEORGIA. MC DUFFIE CO: vicinity of Thomsin, *Bartlett* 1496 (MICH). LUMPKIN CO: Mt. Woods, Frogtown Gap, *Leeds* 1561 (PH). KENTUCKY. WARREN CO: Ky. Rt. 101, n. of bank Barren River at Warren-Allen Co. line, *M. Brown & J. Brown, Jr.*, 4587 (NCU). NORTH CAROLINA. BUNCOMBE CO: Biltmore Herbarium 14954 (RM). CABORRUS CO: branch of Little Buffalo Creek, 2 mi. s. of Rowan Co. line and 3 mi. e. of Watts crossroads, *Ahles* with *Leisner* 19665 (NCU). CLEVELAND CO: near top, King's Mt., *Coker*, May 19, 1919 (NCU). GASTON CO: Crowder's Mt., *Radford & Haesloop* 7080 (NCU). HENDERSON CO: *Rev. J. Davis* 7308 (MO). LINCOLN CO: wooded margin of Leeper's Creek, e. of Iron Station, *Bell* 8885 (NCU). POLK CO: between Tryon and Sluda, *Ashe*, May 23, 1916 (NCU); Tryon, *Peattie* 1372 (NCU). RANDOLPH CO: 1 1/2 mi. n.w. of Randleman, *Melvin*, Sept. 13, 1953 (NCU). STANLEY CO: 4.8 mi. e. n.e. of Albmarab near Little Mt., *Ahles* with *Radford* 11898

(FSU). TRANSYLVANIA CO: Pisgah Forest, *Ashe* 2342 (NCU); 3 mi. s.e. of Breward, *Freeman* 57281 (NCU). SOUTH CAROLINA. CHEROKEE CO: 4.3 mi. s.e. of Cherokee Cleveland Co. line on U. S. Rt. 29, *Ahles* with *Haesloop* 22668 (NCU); 1.4 mi. s. of U. S. Rt. 29A on dirt road along Broad River, *Ahles* with *Haesloop* 31044 (NCU). GREENVILLE CO: summit of Caesar's Head, *Leeds* 1310 (PH). OCONEE CO: dry woods near Jocasse, *Freeman* 59291 (NCU). PICKENS CO: Table Rock State Park, *Freeman* 58164 (NCU); 3.8 mi. n. from U. S. Rt. 178 on Sassafras Mt. Road, *Ahles* with *Bell* 14335 (NCU). SUMTER CO: 6 mi. s. s.w. of Sumter near U. S. Rt. 15, *Radford* 24053 (NCU).

EXCLUDED SPECIES

S. herbacea Thunb. Fl. Cap. ed. Schult, 341 (1823) = *S. salicifolia* Griseb. in Mart. Fl. Bras iii 1. 19 Bras.

S. pseudo-china Bert. ex Kunth, Enum. Pl. V 183 = *S. balbisiana* Kunth, Enum. Pl. V. 183. Ind.

S. pseudo-china Blanco, Fl. Filip. ed. 1, 795 (1837) = *S. blancoi* Kunth, Enum. Pl. V. 262. Philipp.

S. pseudo-china Descourt., Fl. Antill. VII, 47. t. 462 (1829 = (Quid) Ind. occ.

S. pseudo-china Herb. Madr. ex Wall. Cat. n. 5130 = *S. zeylanica* Linn. Sp. Pl. 1029. Ind. or Malaya.

S. pseudo-china Mart. & Gal. ex A. DC. in DC. Monog. Phan i, 87 (1878) = *S. moranensis* Mart. & Gal. in Bull. Acad. Brux. IX, ii (1842) 389. Mexico.

S. pseudo-china Schiede ex A. DC. in DC. Monog. Phan. i, 84 (1878) = *S. cordifolia* Humb. & Bonpl. ex Willd. Sp. Pl. IV. 778. Mexico, Ind.

S. pseudo-china Sieber, ex A. DC. 1. c. 170 (1878) = *S. telferiana* Wall. Cat. n. 5121 A. Ins. Maurit.

S. pseudo-china Gray, Manual of the Botany of the northern U.S. 1848 = *S. hispida* Muhl.

S. pseudo-china Rydb. Fl. Prairies & Plains of Central North America 227 (1932) = *S. hispida* Muhl.

S. pseudo-china Britton and Brown, Ill. Fl. U. S. & Canada. 1: 441 (1896) = *S. hispida* Muhl.

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NEW ENGLAND SALT MARSH VAUCHERIAE

E. E. WEBBER[1]

Prior to 1953, only four species of *Vaucheria* (*V. compacta* (Collins) Collins, *V. litorea* C. Ag., *V. piloboloides* Thur., and *V. thuretii* Woron.) were known from marine and estuarine habitats of northeastern United States (Blum and Conover, 1953). At this time, collections of *Vaucheria* by these authors from salt marshes of the Woods Hole area yielded four additional species. Three of these had not been reported as occurring in North America. They are *V. arcassonensis* Dangeard, *V. coronata* Nord., and *V. intermedia* Nord. The fourth was described as a new species, *V. minuta*. Subsequent collections by Blum (1960) at Essex, Massachusetts resulted in the description of a second new species of *Vaucheria* from New England salt marshes, *V. vipera*.

From the extensive tidal marshes in the immediate vicinity of the Castle Neck River, Ipswich, Massachusetts, several *Vaucheria* species were encountered by the present author, the plant masses appearing as greenish-black "turfs" on mud and sandy-peat substrates. Descriptions and ecological observations of these plants are presented below.

V. intermedia Nord. fig. 1

Plants monoecious, vegetative filaments 15-31μ wide, oogonium spherical to somewhat elongate, 80-110μ diameter and 85-120μ long, opening by a terminal pore, oospores (74μ) 93-110μ diameter and not quite filling the oogonium; antheridia cylindrical, 26-36μ wide by 75-124μ long, opening by 1-3 lateral pores and subtended by what appears to be an empty cell, the antheridium either attached to the oogonium or on a separate branch at the base of the oogonium; vegetatively abundant in June and July, reproductive from September through the winter to early March.

Plants of this species were located in the mud at the seaward edges of the salt marsh, and in the sandy-peat soil

[1]The author thanks Dr. John L. Blum for his preliminary reading of this manuscript.

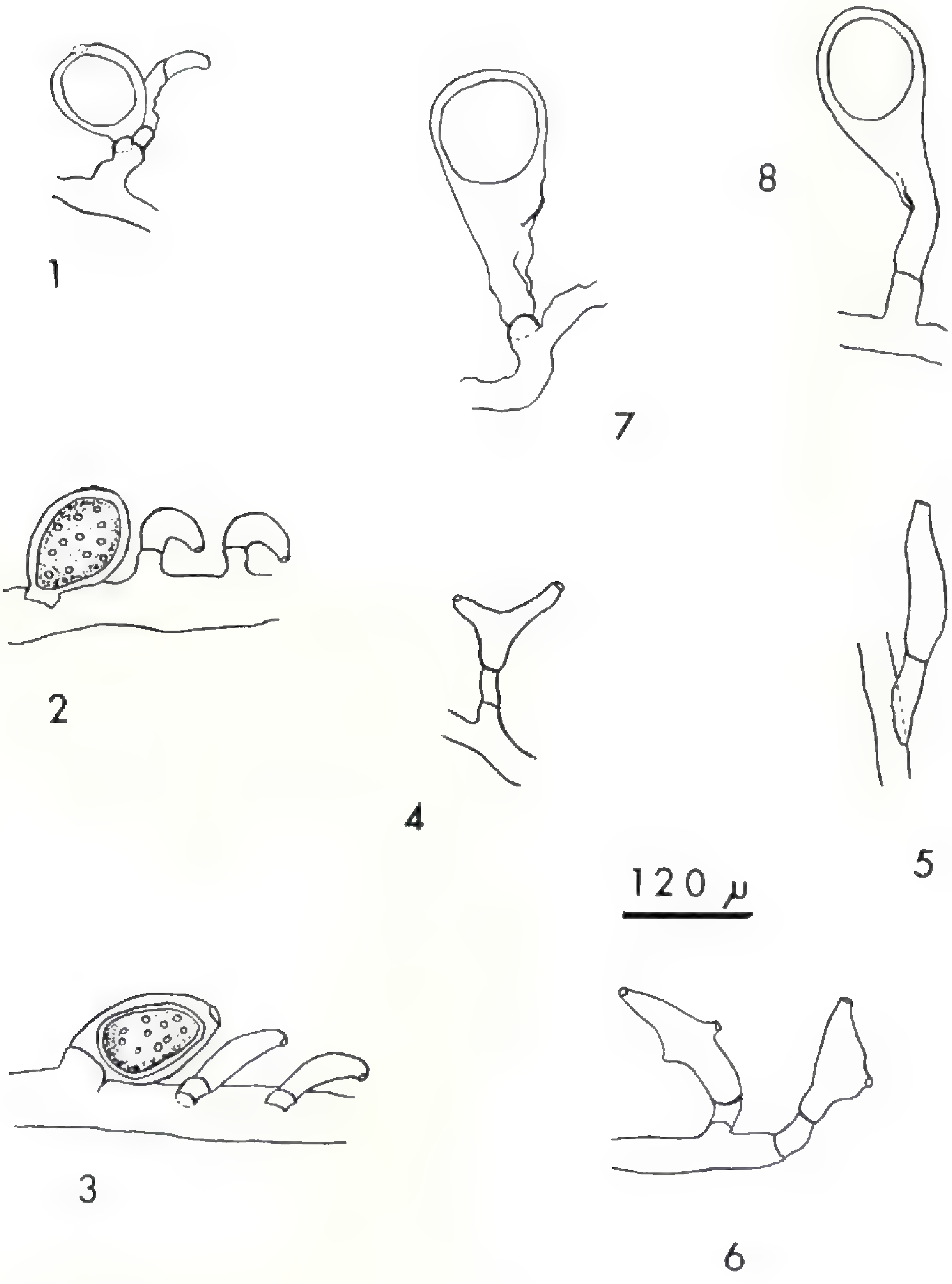

Fig. 1, *V. intermedia,* growth habit of antheridium and oogonium; Figs. 2, 3, *V. arcassonensis,* showing incurved character of both gametangia; Figs. 4-8, *V. compacta* var. *koksoakensis,* variation in antheridial morphology (4-6), and the typically long and terminally enlarged oogonia (7, 8).

at the bases of *Spartina patens* on the surface of the marsh, here admixed with *V. arcassonensis.*

Dangeard (1939) claimed *V. intermedia* as a brackish

water species, while Blum and Conover (1953) noted its ability to withstand a range in salinities from fresh water to sea water of 27°/oo. The latter authors further determined reproduction to occur between a temperature range of 0-18.5°C. The reproductive period of *V. intermedia* from Ipswich coincided with salinities of 17.5-33°/oo along with temperatures varying from -2° to 18°C.

V. arcassonensis Dangeard figs. 2, 3

Plants monoecious, filaments 55-62μ wide, oogonium sessile or short stalked, opening by a terminal pore, oospore ovoid-cylindrical, 80-91μ $\times$ 112-124μ, thick walled, and with many oil droplets, oospore essentially filling the oogonium, antheridia cylindrical, 31μ $\times$ 124μ, discharging terminally, both gametangia often incurved toward the filament; vegetatively abundant from June through August, reproductive during May.

This species formed conspicuous, mat-like expanses in the soil at the bases of *Spartina patens.*

The collections of *V. arcassonensis* by Blum and Conover (1953) are apparently the only record of this species in North America. While actual measurements of their plants are not given, they stated that "they do not seem to differ significantly in any way from the collection reported by Dangeard." In his original description, Dangeard (1939) cited filament widths of 36-54μ and oospores 60-70μ wide and 80-100μ long. Although the Ipswich plants are considerably larger than those reported by Blum and Conover (1953), they do not exceed the range of variability for this species (Blum, pers. comm.).

V. compacta (Collins) Collins figs. 4-8
var. *koksoakensis* Blum and Wilce

Plants dioecious, filaments 31-43μ wide, oogonium 236-550μ long and terminally enlarged, oospores spherical, 105-161μ diameter, antheridia stalked, 31-37μ $\times$ 86-170μ (192μ), subtended by an empty cell and discharging through lateral and terminal papillae (occasionally the papillae may be

lacking), several antheridia often produced per branch, or rarely the antheridium may bifurcate; vegetative in May and June, reproductive from July through November, carpeting the mud of creek banks.

Vaucheria compacta has been reported from Massachusetts salt marshes by Collins (1900) as *V. piloboloides* var. *compacta*. Recently, Blum and Conover (1953) found *V. compacta* in the Woods Hole area. In 1958 Blum and Wilce described a new variety of *V. compacta*, the variety *koksoakensis*, from Ungava Bay, Quebec, where the plants formed "turf-like" expanses on the intertidal mud near the mouth of the Koksoak River. They distinguished this new variety by the much greater length of the oogonium, as compared with that of *V. compacta*. Blum and Conover (1953) found *V. compacta* to be reproductive only during the winter at temperatures below 18.5°C. and salinities less than 27°/oo; however, the Ipswich plants of *V. compacta* var. *koksoakensis* reproduced from July through November, and occurred in environments with temperatures commonly to 25°C. and salinities to 27°/oo.

Thus, it appears that *V. compacta* var. *koksoakensis* is a variety having both morphological features and environmental relationships which distinguish it from *V. compacta*. Further, the collections from the Ipswich salt marsh represent the first record for the presence of *Vaucheria compacta* var. *koksoakensis* in the United States.

DEPARTMENT OF BIOLOGY
KEUKA COLLEGE, KEUKA PARK, N.Y. 14478

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DEVELOPMENTAL VARIABILITY OF CORNUS CANADENSIS IN NORTHERN NEW ENGLAND

JAMES A. TEERI[1]

The forms and varieties of *Cornus canadensis* L. have received considerable taxonomic attention with little resulting unanimity. Fernald (1950) recognized f. *elongata* Peck (". . . pairs of leaves all scattered . . .") and f. *purpurascens* (Miyabe & Tatewaki) Hara. He also listed × *C. unalaschkensis* Ledeb., a hybrid of *C. canadensis* and *C. suecica* L., and stated "Innumerable minor forms have been noted."

Fernald and Wiegand (1911) stated ". . . *Cornus canadensis* L., has the leaves ordinarily closely crowded and appearing whorled at the summit of the nearly naked or only slightly bracted stem." They depicted *C. canadensis* var. *intermedia* Farr. as having one to three pairs of cauline leaves which were well developed and 1/2 to 1/3 the size of the uppermost leaves. At the time they considered var. *intermedia* to be synonymous with *C. unalaschkensis* Ledeb. and noted that in some characters var. *intermedia* resembled *C. suecica* but the two were distinct.

The forma *elongata* is described by Pack (1911) as possessing an elongated stem ". . . bearing a pair of opposite leaves at each of three or four nearly equidistant nodes, or bearing a whorl of four leaves near the base and two or three pairs of opposite leaves above . . ."; he separated this form from *C. suecica* on the basis of the leaf venation.

Arséne (1927) reported a confusing intermediate form of *C. canadensis* on St. Pierre et Miquelon and listed both *C. canadensis* and *C. suecica* as present. Both species were reported from St. Paul Island by Perry (1931), who mentioned observing what was believed to be the hybrid (× *C. unalaschkensis*). Erskine (1956) stated that the hybrid

[1]The author thanks Dr. A. R. Hodgdon for helpful discussion and suggestions.

was found frequently on the same island. Porsild (1939) said that in the rather localized portions of North America where *C. canadensis* and *C. suecica* overlap in range, it is easy to treat var. *intermedia* as a hybrid of the two. But, he cited Fernald as mentioning that in many parts of its range "*Cornus canadensis* L. var. *intermedia* is common or occasional . . . more than a thousand kilometers from the nearest station of *C. suecica*."

The following were listed by Lepage (1946) as synonymous with the hybrid *C. canadensis* L. × *C. suecica* L.: *C. unalaschkensis, C. canadensis* var. *intermedia* and *C. canadensis* var. *alpestris* House. Later Lepage (1950) established the forma *alpestris* based on his collections of plants which had both the typical branch and the f. *alpestris* branch growing from the same rhizome. He called the entire plant f. *alpestris*. Smith and Schofield (1952) found both *C. canadensis* and *C. suecica* growing together abundantly in Cape Breton county, yet they reported the hybrid not present.

Several forms of *C. canadensis* were cited for Minnesota (Lakela, 1948) as ". . . ecological variants differing vegetatively from the typical form. . .".

In 1967, on Mt. Washington, New Hampshire, I collected several plants of what appeared to be *C. canadensis* f. *elongata* with ". . . pairs of leaves all scattered . . ." Fernald (1950). During that summer and fall, further observations of *C. canadensis* in northern New England gave the impression of significant developmental variability. Closer inspection revealed that some of these elongated plants were growing from the same rhizome as adjacent, more typical plants of *C. canadensis* (Fig. 1.). Similar rhizomes with both upright forms were located on the east, south and western slopes of Mt. Washington. The plants occurred primarily between 4,200 ft. and 5,000 ft. above sea level in the zone of spruce-fir scrub. Below this elevation *C. canadensis* occurred primarily as the typical form, although occasional aberrant individuals appeared in all areas of northern New England. Several rhizomes, each bearing the two forms,

PLATE 1381

Fig. 1. A single rhizome of *Cornus canadensis* bearing stems of the typical and elongate forms; collected on Mt. Washington, N.H., about 4,500′ above sea level in spruce-fir scrub.

were collected at West Quoddy Head, Lubec, Maine, at 20 ft. above sea level.

In many locations on Mt. Washington, in addition to mixed colonies, pure colonies of either the elongated form or the typical form were found throughout the scrub zone. Both forms could be found in pure and mixed colonies at the upper altitudinal limit of the species. Stems which developed later in the growing season (late July and August) tended to be of the elongated form; these late-developing plants were usually strictly vegetative. When an inflorescence was present, parts were frequently deformed (i.e. grossly uneven bracts, clustered misshapen peduncles). The opposite cauline leaves varied in size from 1/8 to 3/4 the size of the typical terminal leaves (which also vary considerably in size).

Flowering and vegetative development of many temperate region plants is often correlated with periods of high

temperature during the growing season. Walker (1957), discussing frost injury to garden peas, noted that when an apical meristem was killed, basal dormant buds often responded with elongated internode growth. If lower temperature is to be correlated with abnormal development and failure of flowering in bunchberry, then the most frequent occurrence of aberrant plants would be expected in the cooler parts of the range, along with occasional late-starting aberrants throughout the range. This agrees with the present observations. It is of interest that Peck's (1911) collections of f. *elongata* are both from cool sites "Cranberry marsh, . . . and Averyville marsh . . ." in New York. House (1924) described another morphologic aberrant of *C. canadensis*, var. *alpestris*, as "In both localities growing among rocks beneath which ice persists throughout most of the summer."

The many other possible causes of aberrations cannot be generally excluded and it is doubtless true that other factors, in addition to low temperature, can contribute to the phenotypic confusion of *C. canadensis*. However, the fact that frequent developmental aberrants appear primarily in cool sites in the range strongly suggests the temperature relationship.

Future studies of this group should consider developmental aberrations as well as genetic forms (e.g. color mutants) and hybrids. Plants such as f. *elongata*, which have been consistently found on the same rhizome as the typical form, raise considerable question as to the desirability of assigning a formal name to the variant branch. Perhaps the best treatment is simply to note the occurrence of this sort of variation in the species description.

DEPARTMENT OF BOTANY
UNIVERSITY OF NEW HAMPSHIRE, DURHAM

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MAUD H. PURDY 1874-1965

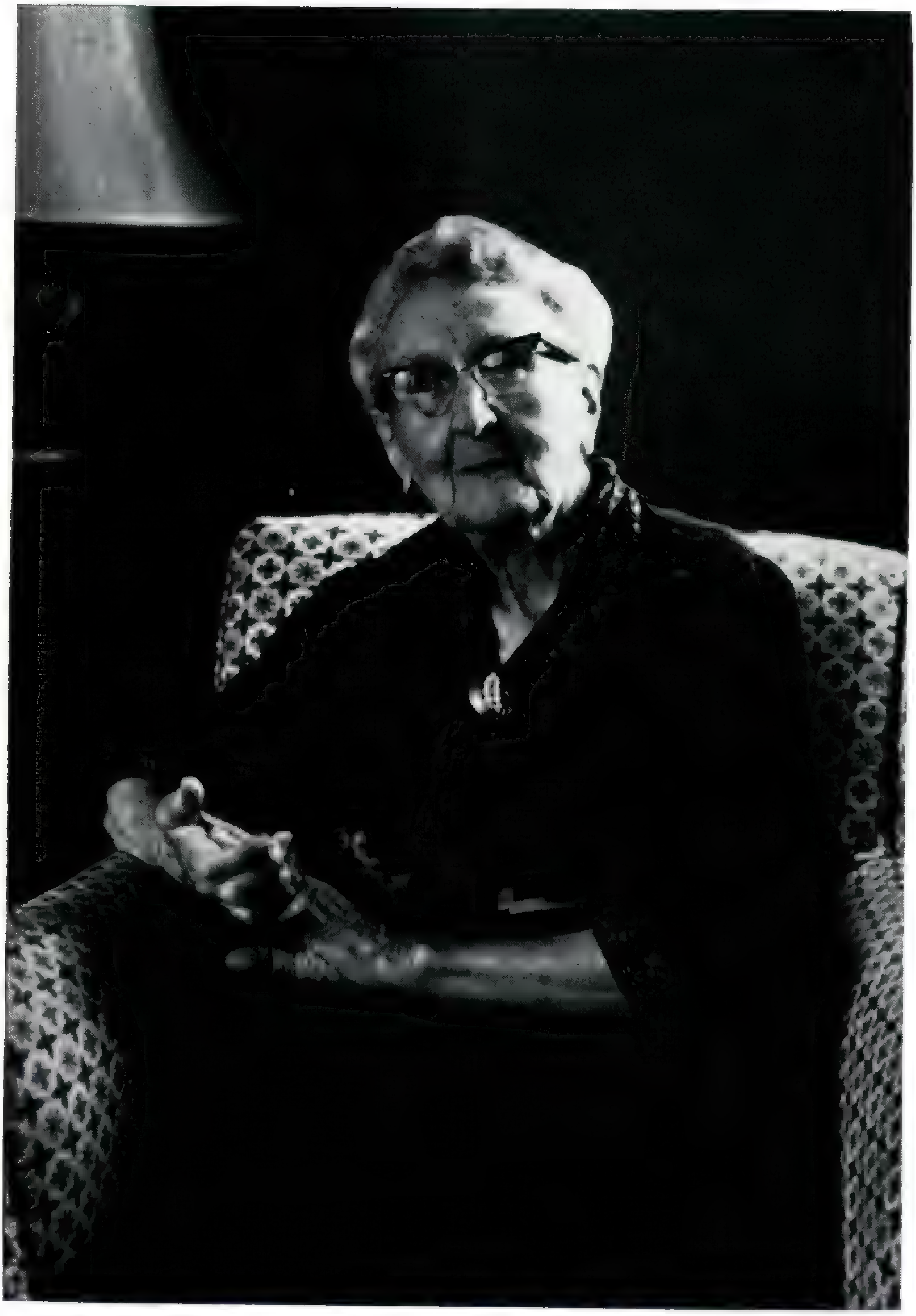
Miss Maud Helena Purdy, miniature painter and botanical illustrator died in June, 1965, at her place at the Pomona Country Club in Rockland County, New York, at the age of ninety-one.

When I first met Maud Purdy, she was a gray-haired vivacious artist of over fifty, with a rather thin figure. She was always a cheerful and most hospitable person, greatly interested in her house and rock garden at Pomona, which she visited week ends and where she stayed all summer. She did not change very much. The accompanying picture, taken in her late eighties, is a good representation.

For garden work and for botanical illustration she had indomitable energy. Like Schuyler Mathews, Miss Purdy was able to bring dead botanical specimens to life, with many variations of line technique to show surface differences. Schuyler Mathews graciously gave me pointers in botanical drawing during his many visits to the Gray Herbarium in the 1920's, but after coming to Brooklyn with Miss Purdy's help I no longer had to attempt botanical illustration.

From childhood Maud Purdy was a trained artist, who later specialized on miniature portraits on ivory. It was through this exacting work that she took naturally to delineation of minute structures in plants. She worked well with a microscope, and would not draw anything unless she could clearly see it. Accordingly she demanded clear dissections of the material to be illustrated.

Maud Purdy was born in Philadelphia, the elder daughter of Dr. Charles G. Purdy and Ellen M. Wildman. When she was at an early age the family moved to the Flatbush section of Brooklyn, — the "Vlackte Bosch" or flatwoods of the Dutch settlers, as was seen from the terminal moraine in Brooklyn. Flatbush was then one of the show places of New York, with spacious lawns and gardens, and large houses set far back from the streets. Dr. Purdy, a prominent physician of this locality, lived in one of these houses.



The Brooklyn Botanic Garden, and the adjacent Prospect Park, occupy the southern slope of the terminal moraine. Nearly everything else of a country aspect is gone.

Weekends and summers Miss Purdy spent at her place in Pomona. To the north her house overlooked Mount Ivy and the Ramapo Mountains. It occupied a crest of the conglomerate rock of the Hudson Valley series, a natural location for a rock garden. This garden was laid out principally by Montague Free, a co-worker at the Brooklyn Botanic Garden. The adjacent rich meadows I remember as abounding in *Trollius laxus* and other calciphile plants. The meadows are now ditched and covered to a large extent by housing projects. Little if anything remains of their appearance a few decades ago. The ravines in the neighborhood had an abundance of the walking-fern and *Allium tricoccum*.

Miss Purdy made illustrations for the various publications of the Brooklyn Botanic Garden, including for me the studies in *Eleocharis*, illustrations of Tennessee plants, and the Vegetation of the Galapagos Islands and the coasts of Ecuador and Peru. She also made a series of water colors of the various species of gentian of northeastern United States and Canada, with the plant and corolla dissection in the foreground and landscape in the background.

Her faithful work on dissections is well seen in Dr. Gundersen's "Families of Dicotyledons". For the School Nature League of New York City, she made under the supervision of Dr. Arthur H. Graves, a series of drawings of American oaks that I think are unsurpassed. These were incorporated in Dr. Graves' "Illustrated Guide to Trees and Shrubs". Miss Purdy had an excellent idea of the appearance of lines in drawings after they were reduced for printing. Many of the drawings in this volume were not reduced, as contemplated, and lines are therefore somewhat heavy.

Miss Purdy belonged to the Spring Valley Methodist Church, and to the local Audubon and Conservation Societies and Garden Clubs, and was a graduate of Adelphi Academy and Pratt Institute in Brooklyn. She is survived

by her sister, Mrs. George H. Tomes of Garden City, New York and by a niece, Mrs. William B. Strong, also of Garden City. She was buried in the West New Hempstead Cemetery in Rockland County.

HENRY K. SVENSON
OSTERVILLE, MASSACHUSETTS 02655

ANOTHER NOTE ON SAGEBRUSH TAXONOMY. When the western, woody species which comprise the more or less natural section Tridentatae of *Artemisia* were studied (Beetle, 1960) a name was overlooked as follows: *Artemisia tripartita* Rydb. var. *hawkinsii* E. H. Kelso Rhodora **39**: 151. 1937.

The type was collected in Yellowstone National Park, Wyoming. This name is synonymous with *Artemisia arbuscula* subsp. *thermopola* Beetle Rhodora **61**: 83. 1959.

This type is from Teton County, just south of Yellowstone National Park and other specimens are cited from the park.

A. A. BEETLE
PLANT SCIENCE DIVISION,
UNIVERSITY OF WYOMING, LARAMIE, 82070

A WHITE FLOWERED FORM OF BAUHINIA COULTERI FROM TAMAULIPAS, MEXICO. During a study of the genus *Banhinia*, section *Bauhina*, a collection of *Bauhinia coulteri* was discovered which had white rather than the usual pink flowers. This color form new to science is here described.

Bauhinia coulteri Macbride forma *albiflora*
Wunderlin, forma nova.

A forma *coulteri* recedit floribus albidis.

Presently known only from the type collection.

Type: In broad dry arroyo 19 km SE of Miquihuana on road to Palmillas, Tamaulipas, Mexico, "arroyo filled with

Acacia, Mimosa, and *Salvia,* fls. white," 11 Aug. 1941, *Stanford, Retherford,* and *Northcraft 851* (MO).

R. P. WUNDERLIN
DEPARTMENT OF BOTANY,
SOUTHERN ILLINOIS UNIVERSITY, CARBONDALE, 62901

SOLIDAGO GYMNOSPERMOIDES IN ILLINOIS

Fernald (1950) and Gleason (1952) include Illinois in the range for *Solidago gymnospermoides* (Greene) Fern. Jones and Fuller (1955) state that the Illinois plants have been misidentified and are really *Solidago media* (Greene) Bush, thus excluding it from the Illinois flora. This interpretation has been followed by other authors regarding the Illinois flora to date. *Solidago gymnospermoides* differs from *Solidago media* in having leaves 1-nerved, sometimes faintly 3-nerved, conspicuously puncticulate, and with heads cylindric, tending to be pedicellate while *Solidago media* has leaves 3-nerved, usually with 1-2 additional pairs of fainter nerves, punctation not conspicuous, and with heads slenderly campanulate or turbinate, chiefly sessile or subsessile in small glomerules. The western ranging *Solidago gymnospermoides* does extend into northern and west-central Illinois and appears to be common in dry situations there. Because of its close resemblance to *Solidago media* it apparently has been overlooked and misidentified as this species. The following two specimens deposited in the herbarium at Southern Illinois University are cited as representative specimens as proof of this species in Illinois: MASON CO.: Near Tehron, *Winterringer 5046;* WILL CO.: Along New York Central Railroad between Frankfort and Will-Cook County line, *Schulenberg, Schauss, & Kopp s.n.* Specimens in other herbaria have also been examined by the author from Cass, Cook, Kanakee, and Stark Counties.

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R. P. WUNDERLIN
DEPARTMENT OF BOTANY
SOUTHERN ILLINOIS UNIVERSITY
CARBONDALE, ILLINOIS 62901

THE DIAGNOSTIC VALUE OF FRESH MATURE DRUPES OF VIBURNUM RECOGNITUM AND V. DENTATUM In the company of H. K. Svenson and J. A. Churchill on September 12, 1967, I collected *Viburnum recognitum* Fern. and *V. dentatum* L. growing side by side at two widely separated places in Barnstable County, Massachsetts, near the northern limit of range for the latter species. The cymes of blue-black fruit were abundant.

The two species were easily distinguished at a distance of several meters one from the other by their foliage, the leaves of the former being relativly small, elliptical and acute to acuminate. On close inspection, the fruits were distinctive. Those of *V. recognitum* were globose with short pointed style bases surmounting the flattish summits, and measuring 5-6 mm long exclusive of the points. In marked contrast, the fruits of *V. dentatum* were ellipsoid with somewhat longer points and 6-7 mm long. No intergrades were noticed at either station.

Curiously, Fernald (1), (2), makes no mention of fresh ripe-fruit characters of these two species aside from color. Gleason (3) makes no reference to *Viburnum recognitum* as a taxon of any rank, and confines his description of the drupes of *V. dentatum* to the statement ". . . . blue-black, subglobose to ovoid, 5-10 mm long." McAtee (4) describes those of *V. recognitum* var. *recognitum* as "spherical to ovoid, 4 to 6 (usually 5) mm. in length (dried) ; and those of *V. dentatum* "spherical to ovoid, 4 to 6 mm. long (dried)." Apparently, he had observed no difference in shape of fresh fruit between the two.

I call attention to the possibility that the size and shape of mature fresh fruit may prove to be of diagnostic value.

Herbarium and pickled material have been prepared bearing the following collection data: —
Viburnum recognitum Fern. Roadside thicket, East Sandwich, Barnstable County, Mass., 12 Sept. 1967, *Eaton 6079*, margin of Hoxie Pond, E. Sandwich, 12 Sept. 1967, *Eaton 6083*.

Viburnum dentatum L. (same as *6079*), *Eaton 6080*; (same as *6083*), *Eaton 6082*.

RICHARD J. EATON
LINCOLN, MASSACHUSETTS 01773

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A RANGE EXTENSION FOR HUDSONIA ERICOIDES IN THE SOUTHEASTERN UNITED STATES. The following note contains new distributional data for *Hudsonia ericoides* L., Golden-Heather. *Hudsonia ericoides* was reported by Small (1933) as occurring from North Carolina to Nova Scotia. Fernald (1950) indicated a similar distribution, but stated that the North Carolina record needed verification. Brizicky (1964) also noted that this report was dubious. Due to the absence of herbarium material to substantiate the previous reports this species was excluded by Radford, *et al* (1964) from the Carolinas' Flora.

On May 5, 1967, the authors found *Hudsonia ericoides* L. growing on a low sand hammock, east of Juniper Creek near U.S. highway 1, Chesterfield County, *South Carolina*. This collection established the occurrence of *H. ericoides* in the Carolinas' Flora and also establishes a new record for the state of *South Carolina*. Several hundred plants were noted during a subsequent search of the area on May 25.

The population of *Hudsonia ericoides* L. occupies an area approximately 300 yds. in length and 75 yds. in width.

Sand from the well leached white sand hammock has been removed for construction purposes leaving pits scattered throughout. These excavations range to 10 ft. in diameter and 2-3 feet in depth, which approximates the water table. *Hudsonia* is most abundant around the rims of some of these excavations. In other excavations the bottom is wet enough to provide a suitable habitat for a number of pine-savannah species.

Several species of interest were found associated with the above population of *Hudsonia ericoides* L. The dominant ground cover consisted of *Cladonia* spp., *Selaginella arenicola* ssp. *acanthonota* (Underw.) Tryon, *Tradescantia rosea* var. *graminea* (Small) Anderson, *Polygonella polygama* (Vent.) Engelm. & Gray, *Arenaria caroliniana* Walt., *Stipulicida setacea* Michx., and *Solidago pauciflosculosa* Michx. The dominant trees were *Pinus palustris* Miller, *Quercus laevis* Walt., *Q. incana* Bartram, and *Q. margaretta* Ashe. All of the above species characterize xeric sites in the Carolina Fall-line sandhills (Wells and Shunk, 1931; Duke, 1961) and follow a definite distributional pattern through this area (Radford, *et al*, 1965).

Certain species of more mesic tolerances were also found growing on the hammock: *Pinus serotina* Michx., *Magnolia virginiana* L., *Leiophyllum buxifolium* (Bergius) Ell., *Vaccinium crassifolium* Andr., *Ilex glabra* (L.) Gray, *I. coriacea* (Pursh) Chapm., *Cyrilla racemiflora* L. and *Clethra alnifolia* L. The occurrence of the above species here is indicative of a high water table. *Leiophyllum buxifolium* was observed to be very abundant here and at other similar but scattered localities in the Coastal Plain.

This association with *Leiophyllum buxifolium* (Bergius) Ell. is of particular phytogeographical interest since there are parallels in the infra-specific or specific distribution (depending on interpretation of present information) of *Leiophyllum* and *Hudsonia*. *Leiophyllum buxifolium*, treated as a single species by Radford, *et al* (1964-1965), has two varieties in the Carolinas (Wood, 1961). A disjunct var. *prostratum* (Louden) Gray is restricted to the Smoky

and Blue Ridge Mountains, while a closely related var. *Hugeri* Schneider occurs both in the Coastal Plain and Mountains with two stations between. *Hudsonia montana* Nutt., endemic to the mountains of North Carolina, exhibits a similar disjunct pattern with *H. ericoides*. It is interesting to speculate as to whether or not these patterns were formed simultaneously by the same or similar factors. Several other species, such as *Kalmia angustifolia* var. *caroliniana* (Small) Fern., *Gaylussacia dumosa* (Andrz.) T. & G., *Vaccinium corymbosum* L., *Hypericum canadense* L., and *H. densiflorum* Pursh, would be important in the determination of these factors, since they show similar distributional patterns (Radford, et al, 1965).

Assuming an affinity for the same ecological requirements or niche, several unsuccessful searches for additional populations of *Hudsonia ericoides* L. have been made of known *Leiophyllum* localities in the Coastal Plain of the Carolinas. The possibility of *Hudsonia ericoides* having been planted in South Carolina seems remote, and even so, the species appears to be well established. Specimens are being distributed to major herbaria (Bozeman and Logue 9126, 9176).

JOHN R. BOZEMAN AND JOHN F. LOGUE
DEPARTMENT OF BOTANY,
UNIVERSITY OF NORTH CAROLINA, CHAPEL HILL, 27514

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TWO NATURALLY OCCURRING ABNORMALITIES OF THE DIATOM PODOCYSTIS ADRIATICA.[1 2] While frustular aberrations of diatoms are common in cultures (2, 5), they are uncommonly observed in natural samples. This paper describes two abnormal forms of the epiphytic diatom *Podocystis adriatica* (Kütz.) Ralfs.

During a routine examination of Rhode Island marine algae for epiphytic diatoms, a fertile female specimen of *Grinnellia americana* (C.Ag.) Harv. was observed to harbor several scattered brown clusters of diatoms. After oxidation of the material with nitric acid, washing with distilled water, and mounting in Hyrax, the diatoms proved to be exclusively *Podocystis adriatica*. Among the several normal cells were occasional occurrences of the abnormality shown in fig. 1-A and one specimen of the abnormality in fig. 1-B (normal frustules are shown in fig. 1-C, D, E). These aberrations correspond to the "marginal" and "surface-pattern" abnormalities described by Conger (1).

The cause of marginal deformities (fig. 1-A) has been attributed to crowding of the cells (2) and to sudden chemical environmental changes (1). The surface-pattern deformity (fig. 1-B), in this case being expressed as an anastomosing and poorly defined pseudoraphe in the upper portion of the frustule, is believed to be a result of disturbance in the formative stages (1). A surface abnormality involving the raphe canal in *Surirella*, was induced by continuous light exposure (2). These abnormalities were thought to occur during auxospore formation (3) but Conger (1) contends that most of them are initiated during the vegetative phase.

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[1]Lamont Geological Observatory Contribution No. 1182.
[2]This research was supported by the G. Unger Vetlesen Foundation.

What appears to be the same deformity as in fig. 1-B was described by Meister (4) as *P. spathulata* forma *anastomosans* from Sumatra (Island Sabang) material, but these forms probably have no taxonomic validity.

It cannot be determined what was the cause of these abnormalities. Since the host plant was below the level of

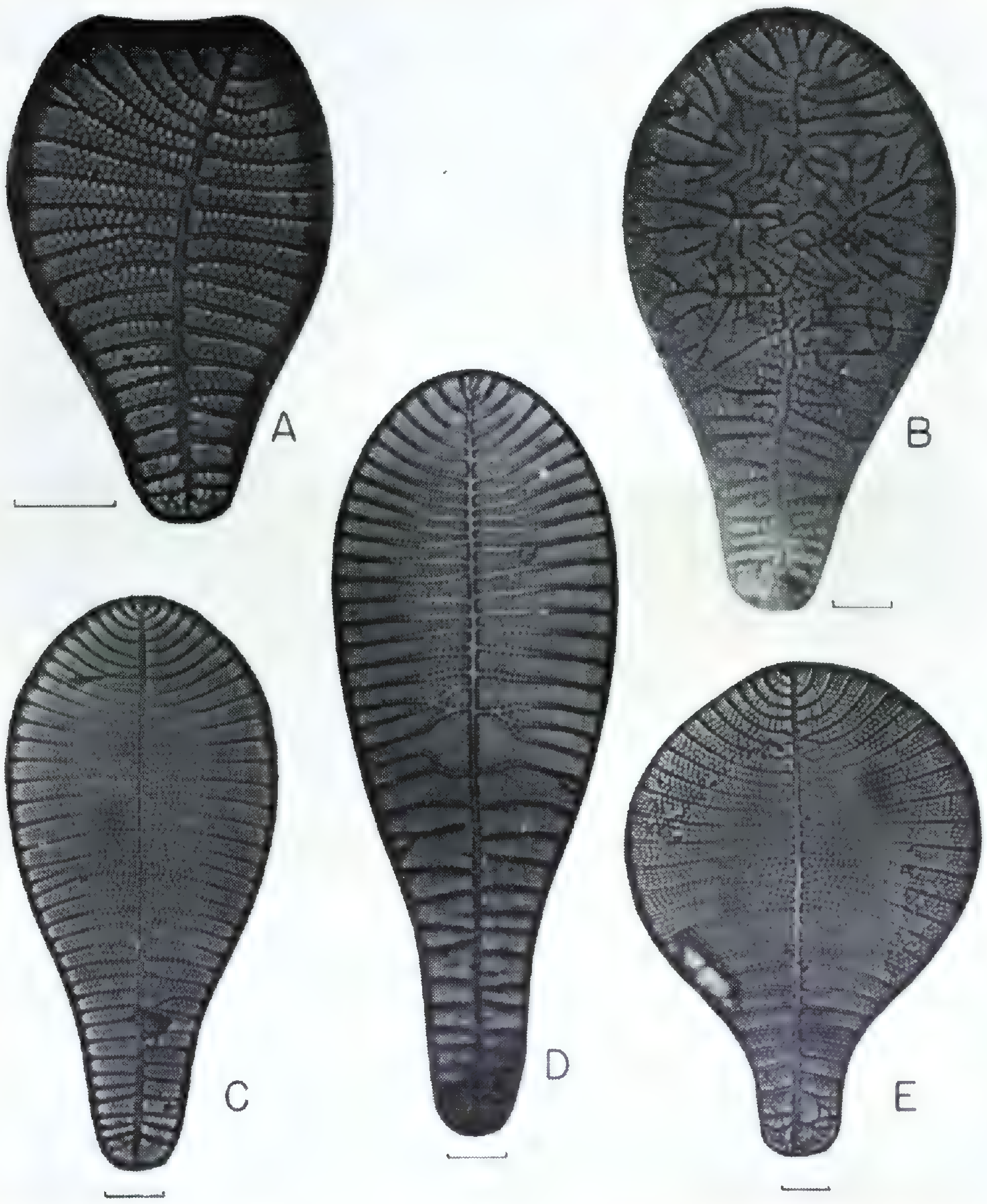

Fig. 1, Plate 1383. *Podocystis adriatica* (Kutz.) Ralfs (A) Marginal deformation; (B) Surface-pattern deformation; (C-E) Variations of normal frustules.
(length of lines is 10u)

spring tides, a sudden exposure to atmospheric conditions is improbable. Neither did there appear to be undue crowding of the frustules on the host. Specimens attached to adjacent *Grinnellia* plants did not exhibit frustule abnormalities. Presumably the initiatory factor for these aberrations was localized.

PAUL E. HARGRAVES
LAMONT GEOLOGICAL OBSERVATORY
COLUMBIA UNIVERSITY, PALISADES, NEW YORK, 10964

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A CASE OF ALBINISM AND OF PRESUMPTIVE SELF-COMPATIBILITY IN ULMUS L.

In late spring of 1964, large numbers of albino elm seedlings were noticed beneath an elm tree located near the northeast corner of Phillips Brooks House, Harvard Yard, Harvard University, Cambridge, Massachusetts. A quick count of normal and albino seedlings indicated approximately three times as many normal green seedlings as albino seedlings, the 3:1 ratio characteristic of progenies derived from self-pollination of individuals heterozygous for single gene recessive albinism. Time did not then permit a more detailed study.

On June 17, 1966 this elm tree was again visited. The ground beneath was well covered with new seed, some of

which had sprouted. Again albinos were observed in great numbers. Unsprouted seed was taken from the ground and, to guard against contamination by seed blown in from other trees, more seed was taken from the little still remaining on the tree.

Germination checks of these two seed lots gave the following results:

	Actual ratio	Predicted 3:1 ratio
Seed from ground —		
Normals	131	129
Albinos	41	43
Total	172	172
Seed from tree —		
Normals	51	49.5
Albinos	15	16.5
Total	66	66

Chi-square tests for both seed lots, though hardly necessary to test such close approximations of the theoretical, indicate a very close fit indeed for a 3:1 ratio.

When germinated in reduced light, the mutant seedlings were pale green. In normal light this color bleached rapidly and it never appeared in seedlings germinated in normal light.

The parent elm is presumably a cultivar of European origin, either a form of *Ulmus glabra* Huds. or possibly the related *Ulmus x hollandica* var. *Klemmer* (Gillekens) Rehder, of Belgian origin, a putative derivative of hybridization of *Ulmus glabra* and *Ulmus carpinifolia.*

In 1946 L. P. V. Johnson reported that his experiments and observations indicated that *Ulmus* species were highly self-sterile. More recently, in 1960, S. P. K. Britwum, finding no seed (with one exception attributed to pollen contamination) on branches bagged before pollination concluded that *Ulmus wilsonii, U. glabra, U. laevis, U. japonica, U. carpinifolia, U. x hollandica, U. thomasii, U. alata,* and *U. americana* were all highly self-sterile.

Several other trees of the same cultivar and elms of other

species are located near the tree of interest here. No albino seedlings were observed in the vicinity of these trees, though normal seedlings were present. The mutant tree is unusual in that it bears a large witches' broom in the upper crown. This abnormality is probably unrelated to the mutant condition, but may possibly be of importance in facilitating self-pollination.

In April, 1967, flowering buds were few and none were observed in the witches' broom. On cut branches brought indoors the main pollen shed occurred one or two days before the stigmas expanded, but some pollen continued to be shed during the period of receptivity of the stigmas.

The data available suggest that this elm tree was largely or entirely self-pollinated and was self-fertile.

SHERRET S. CHASE
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

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NOTE ON CORYDALIS BULBOSA On 2 May, 1932, E. J. Palmer collected a *Corydalis* in the Arnold Arboretum on a "shaded bank, near the new [Bussey] greenhouse and State Laboratory, No. 40005". This was identified as *Corydalis bulbosa* (L). DC., and so listed in the "Supplement to the Spontaneous Flora of the Arnold Arboretum" Jour. Arnold Arb. **16**:92 (1935). This population has persisted to the present. During the first week in May of the present year (1967) it made a considerable show under a tree of the flowering crab *Malus* 'Prince Georges' (AA No. 282-43-A). Collections of flowering and fruiting material were made (DeWolf Nos. 1883 and 1883a) and on checking the identification it was found that the population in fact repre-

sents the species which is currently called *Corydalis solida* (L.) Swartz in European treatments.

It is of interest that, although *Corydalis bulbosa* has persisted for at least 35 years in the same general location, it is still found mostly in the cleared soil under the various flowering crabapples on the bank. It does not seem to be able to spread in competition with the adjacent grasses. Neither has it been able to spread laterally along the hillside into the cleared soil under the shrubs of the *Forsythia* collection. This in spite of an apparently abundant set of fruit.

A note on the name *Corydalis bulbosa* is in order. In 1753 Linnaeus (Sp. Pl. 2:699, 700) recognized a *Fumaria bulbosa* with three varieties: *α cava; β intermedia; γ solida.* These three varieties have been generally treated, by subsequent authors, as distinct species. They have had a varied nomenclatural history, first in *Fumaria* and later in *Corydalis.* In *Flora Europa* (which may be taken as the consensus of European opinion) 1:253, 254 (1964) *α cava* is treated as *Corydalis bulbosa* (L.) DC., *β intermedia* as *C. intermedia* (L.) Merat, and *γ solida* as *C. solida* (L.) Swartz. However, G. Bunting, in a recent article (Baileya 14(1):41-44. 1966) has given convincing arguments, which are summarized below, for a different usage of the names.

The first person to treat the constituent parts of Linnaeus' *Fumaria bulbosa* as distinct species was Philip Miller in the 7th and 8th editions of the Gardener's Dictionary. In the 8th edition he associated the epithet "cava" with the form Linnaeus had treated as *α cava* and the epithet "*bulbosa*" with the form Linnaeus had called *γ solida.*

In 1771, in the 6th edition of the Abridgement of the Gardener's Dictionary, Miller changed his mind and attached the epithet bulbosa to *α cava* and the epithet *solida* to γ solida. It is this altered usage that has been followed by many subseqent authors.

The Code and Rules have been uniformly emphatic that a name must not be changed simply because another name

is more appropriate or familiar. It is clear that Miller's original 1768 publication must be followed.

According to the Flora Europa treatment our plant is to be called:

Corydalis solida (L.) Swartz, ssp. *solida.*

The correct citation following Bunting, for our plant is: *Corydalis bulbosa* (L. emend. P. Miller) DC. in Lam. and DC. Fl. Franc. 4:637, 1805, non Pers. 1807.

GORDON P. DEWOLF, JR.
ARNOLD ARBORETUM OF HARVARD UNIVERSITY
JAMAICA PLAIN, MASSACHUSETTS

ALYSSUM (CRUCIFERAE) INTRODUCED IN NORTH AMERICA

THEODORE R. DUDLEY

The annual species of *Alyssum*, *A. alyssoides* (L.) L. [syn. *A. calycinum* L.] and *A. desertorum* Stapf [syn. *A. minimum* Willd. - non L.] are well-known Old World introductions in the North American flora. Assigned to Section Psilonema and native to much of Europe and Asia, *A. alyssoides* is naturalized in the Argentine and Quebec. In the United States, it is naturalized in Maine, Vermont, Massachusetts, Rhode Island, Connecticut, New York, Pennsylvania, West Virginia, Virginia, Michigan, Indiana, Illinois, Wisconsin, Montana, Colorado, Idaho, Wyoming, Utah, California, Oregon, and Washington. Another native of Europe and Asia, but belonging to Section Alyssum, is *A. desertorum*, which has a much narrower distribution in the United States. It has been collected only from sporadic populations in Bannock County, Idaho; Missoula County, Montana; Sheridan County, Wyoming; and San Juan County, Utah. Frequently confused in American herbaria with *A. alyssoides*, *A. desertorum* is easily distinguished by its larger and glabrous silicles, and early deciduous sepals. The sepals of *A. alyssoides* are persistent, and its silicles always possess an indumentum of stellate hairs.

Material carrying the name *Alyssum maritimum* (L.) Lam., a plant widely naturalized in many states, should be redetermined as *Lobularia maritima* (L.) Desv. Similarily, adventive specimens of *A. petraeum* Ard. and *A. saxatile* L. should be redetermined as *Aurinia petraea* (Ard.) Shur and *Aurinia saxatilis* (L.) Desv., respectively.

Three taxa in Section Alyssum previously unrecorded for the North American flora, *Alyssum szowitsianum* Fischer & A. Meyer, *A. minus* var. *micranthum* (A. Meyer) Dudley and *A. strigosum* Banks & Solander subsp. *strigosum* were recently discovered in the Dudley Herbarium (DS), Stanford University.

A. szowitsianum Fischer & A. Meyer, Ind. Sem. Hort. Petrop. 4: 31. 1837.
Utah. Salt Lake County, Salt Lake City, waste ground above gully, between 14 East Street and 17 South Street, 5 May 1944, *A. O. Garrett s.n.; ibid.*, 26 May, 1944, *A. O. Garrett 8708; ibid.*, dry unoccupied city lot, near ravine, 14 South Street near 18 East Street, 26 May 1944, *A. O. Garrett 8708* (previously determined as *A. alyssoides*).

A. minus (L.) Rothm. var. *micranthum* (A. Meyer) Dudley, Jour. Arnold Arb. 45(1) : 67. 1964.
Colorado. Jefferson County, Golden, waste places, el. 5600 ft., 18 May 1940, *J. H. Ehlers 7985* (previously determined as *A. campestre*). Utah. Salt Lake County, Salt Lake City, near ravine, 23 April 1944, *A. O. Garrett 8675.* California. Modoc County, roadside 2.6 miles north of Buck's Creek Ranger Station, east side of Goose Lake, 13 June 1961, *Ira L. & Dorothy Wiggins 16468.* (previously determined as *A. alyssoides*).

A. strigosum Banks & Solander in Russell, Fl. Aleppo 2: 257. 1794.
California. Santa Clara County, Santa Cruz mountain peninsula, Sierra Azul, west of Mt. Umunhum, el. 3300 ft., 8 May 1920, *H. R. Davis 108* (previously determined as *A. calycinum* & *A. alyssoides*).

Alyssum szowitsianum is well distinguished from all other

naturalized species of *Alyssum* in the United States by having extremely asymmetrically inflated and pubescent silicles. These silicles are tightly adpressed to one another in spike-like infructescences of variable lengths at maturity. This and five other species in Section Alyssum possess an unusual hygrochastic and ombrochorous[1] method of fruit dehiscence and seed dispersal. In the presence of rain, the hygrochastic tissue in the pedicel causes the silicles to move from an ascending or vertical and adpressed position to a spreading or horizontal orientation. In this position, the impact of the rain drops loosens and washes the silicle valves and mucilaginous seed to the ground.

Although closely related in Section Alyssum, *A. minus* var. *micranthum* and *A. strigosum* may be distinguished from each other by the differences in their silicle indumentum. The dimorphic indumentum of *A. strigosum* consists of tuberculate, long bifurcate and erect hairs intermixed with appressed stellate hairs. However, the silicles of *A. minus* var. *micranthum* are covered with monomorphic stellate hairs only, although the unequal lengthed radii may be ascending or erect. Both species illustrate an ombrochorous (without hygrochasty) method of fruit dehiscence and seed dispersal. By this method, the pedicels are brought into a more or less horizontal position early in development. At maturity, the separation tissue between the valves is poorly developed and the mechanical effect of the rain loosens the valves and mucilaginous seeds from the replum.

U.S. NATIONAL ARBORETUM
WASHINGTON, D.C. 20250

[1]cf. Zohary, Palestine Jour. Bot., Jerusalem Series — 1: 151. 1941; op. cit. 2: 125. 1941; op. cit. 4: 158. 1948; op. cit. 4: 239. 1949.

APPLICATION OF THE NAME, HETEROTHECA VISCIDA

VERNON L. HARMS[1]

Asa Gray's (1884) original description of *Chrysopsis villosa* var. *viscida* cites four collections — viz. *Jones, Greene, Pringle,* and *Lemmon.* These syntypes at the Gray Herbarium, Harvard University, were found to represent a heterogeneous assemblage of forms belonging to three different species of the *Heterotheca (Chrysopsis) villosa* complex. The following lectotype was chosen from this syntype series by the author, providing an available epithet for a rare, seldomly recognized, but apparently quite distinct species of the American Southwest, LECTOTYPE "Clefts of dry ledges, Santa Rita Mountains, Arizona, elev. 7500 feet, May 28, 1881, *C. G. Pringle* (GH).

As presently interpreted on the basis of the above lectotype, *Heterotheca viscida* is an uncommon entity of southern Arizona, New Mexico, Trans-Pecos Texas, and northern Mexico. The species apparently does not extend to either northern Arizona or Utah, as Gray's (1884) original description indicates, nor does it reach Colorado as Rydberg (1906, 1917), and Harrington (1954) report. The nearest affinities of *H. viscida* lie with the polytypic species, *H. fulcrata,* from which it differs principally in its distinctly pedunculate-appearing heads, broad obovate or elliptical leaves which are copiously covered with stipitate resin glands but only sparsely hispid along veins, and shorter petioles of lower leaves. Of special interest since the merger of *Chrysopsis* and *Heterotheca* (Shinners, 1951; Harms, 1965), *H. viscida* is the species within the *H. villosa* complex which most closely approaches sect. *Heterotheca (Heterotheca* s. str.*)* in foliage and general pubescence characters.

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[1]Study conducted in part during tenure of National Science Foundation Cooperative Graduate Fellowship at the University of Kansas, and partly supported by National Science Foundation Institutional Grants to University of Alaska #GU-132 and GU-1161. Thanks are due to the cited herbaria for kindly lending materials used in this study.

Heterotheca viscida (A. Gray) Harms, comb. nov. *Chrysopsis villosa* (Pursh) Nutt., var. *viscida* A. Gray, Syn. Fl., 1^2:123. 1884. *C. viscida* (A. Gray) Greene, *Erythea* 2:105. 1894. Perennial taprooted herbs with thick, woody caudices; stems several to numerous, decumbent to erect, 1-3 dm. tall, more-or-less branched; primary pubescence of stems long hirsute-hispid to 2 mm., often sparse, and the secondary pubescence densely stipitate-glandular and short puberulent; leaves densely stipitate-glandular, sparsely hispid at least on veins; lower stem leaves broadly spatulate, with petioles shorter than 2 cm.; middle and upper leaves obovate to broadly elliptic or oblong, 15-40 mm. long, 7-25 mm. wide, usually about twice as long as broad, with sessile blades obtusely based to cordate-clasping; heads distinctly pedunculate with peduncular leaves distant and scarcely reduced, or else the uppermost abruptly narrower than those below; inflorescence open-cymose with a few large heads; involucres turbinate to hemispherical, (7-) 8-12 (-15) mm. wide, 7-12 mm. high; phyllaries linear-lanceolate, the inner about 3 times longer than the outer, outer phyllaries densely stipitate-glandular, sparsely strigose-hirsute to glabrate; rays 8-15 mm. long; disk corolla tubes 5-7 mm. long; inner pappus bristles 4.5-7 mm. long; outer pappus conspicuous, of irregular, narrow-lanceolate, fimbriate squamae, 0.5-1.5 mm. long; achenes 3-4 mm. long, sericeous. Rare on rocky slopes, ledges, and igneous soil at higher elevations in mountains of Trans-Pecos Texas to southern Arizona.

REPRESENTATIVE SPECIMENS

ARIZONA. COCHISE CO.: Chiricahua Natl. Monument, *O. M. Clark 8178* (OKLA); Carr Peak, Huachuca Mts., *L. N. Goodding 210* (OKLA). SANTA CRUZ CO.: Santa Rita Mts., *C. G. Pringle May 28, 1881* (GH). TEXAS. CULBERSON CO.: Guadalupe Mts., *W. V. Fisher August 13, 1950* (OKLA); *C. L. & A. A. Lundell 14390* (SMU); *B. L. Turner 1253* (SMU). JEFF DAVIS CO.: Davis Mts., *D. S. Correll 13540* (SMU); *D. S. Correll 33760* (LL); *L. C. Hinckley 9-29-34* (TEX); *L. C. & L. Hinckley 196* (SMU); *E. J. Palmer 31955* (TEX); *E. J. Palmer 34363* (LL); *B. C. Tharp 3775* (TEX); *B. H. Warnock 6495* (SMU); *M. S. Young 9-13-18* (TEX). PRESIDIO CO.: Chinati Mts., *L. C. Hinckley 2563* (SMU, LL); *R. McVaugh 7463* (SMU, LL).

UNIVERSITY OF ALASKA
COLLEGE, ALASKA 99701

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ALLIUM AMPELOPRASUM L. IN ALABAMA — In 1962 I noted an *Allium* growing along the roadside of US 80 at Faunsdale, Marengo County, Alabama. During several succeeding years I observed this colony a number of times and noted that it was increasing in size. In May, 1967, I collected specimens (Jones 12433) and identified the species as *Allium ampeloprasum L.* Therefore, Alabama is the eighth state (Alabama, Illinois, Kentucky, Mississippi, North Carolina, South Carolina, Tennessee, and Virginia) in the eastern United States in which this species is known to be established. Pullen* reported that this plant occurs in Mississippi and summarized the distribution records in the eastern United States for this species; therefore, I will not elaborate on them here. A voucher specimen of the Alabama record has been deposited in the University of Georgia Herbarium.

I have also collected this plant in a number of counties in Mississippi in connection with the Mississippi Flora Project and vouchers have been deposited in the herbarium of the University of Mississippi. In Jefferson County, Mississippi on the loess bluffs near Church Hill, Bob Noble and I observed several colonies an acre or more in size growing in pastures. *Allium ampeloprasum*, therefore, is definitely able to compete successfully in our regional flora and has clearly become established as a part of it.

SAMUEL B. JONES, JR.
DEPARTMENT OF BOTANY, UNIVERSITY OF GEORGIA,
ATHENS 30601

*Pullen, T. M. 1967. *Allium ampeloprasum* in Mississippi. Rhodora **69**: 61-62.

CHAFF ON THE RECEPTACLE OF SOLIDAGO JUNCEA[1, 2]

Gary H. Morton

While critically analyzing a population sample of *Solidago* from an old field in Bucks Co., Pennsylvania, I noticed that some of the specimens had chaffy receptacles. This character is contrary to the genus description in both of the manuals that pertain to the plants of Northeastern United States. Cronquist, in Gleason (1952), describes the receptacles as, ". . . small, flat or a little convex, naked, alveolate, in a few species becoming fimbrillate." Fernald, in Gray's Manual (1950), says the receptacles are, ". . . small, not chaffy."

It is hard to understand why this character has not been previously reported. One possible explanation is that the receptacle is small. In dry material the chaff readily separates from the receptacle while removing the flowers. This result produces the appearance of a naked receptacle. If one is careful, however, it is possible to remove a disk flower and have chaff remain clasping to the base of the achene as in figure 1-A. The character is best seen by observing a young head. The chaff will protrude through and above the flowers as in figure 1-B. When a comparison with the innermost series of phyllaries is made, the chaff is seen to be very similar in size and texture, but the lower one-half of it is more or less conduplicate, while that of the phyllaries is more or less flat.

[1]I am grateful to Arthur Cronquist for his helpful suggestions after reading the manuscript. Work on this paper was carried out with the support of a Title IV NDEA fellowship.

[2]Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. 307.

The group of specimens with chaffy receptacles were keyed to *Solidago juncea* Ait. Material labeled *S. juncea* in the herbarium of the University of Tennessee was checked and it was found to possess chaff.

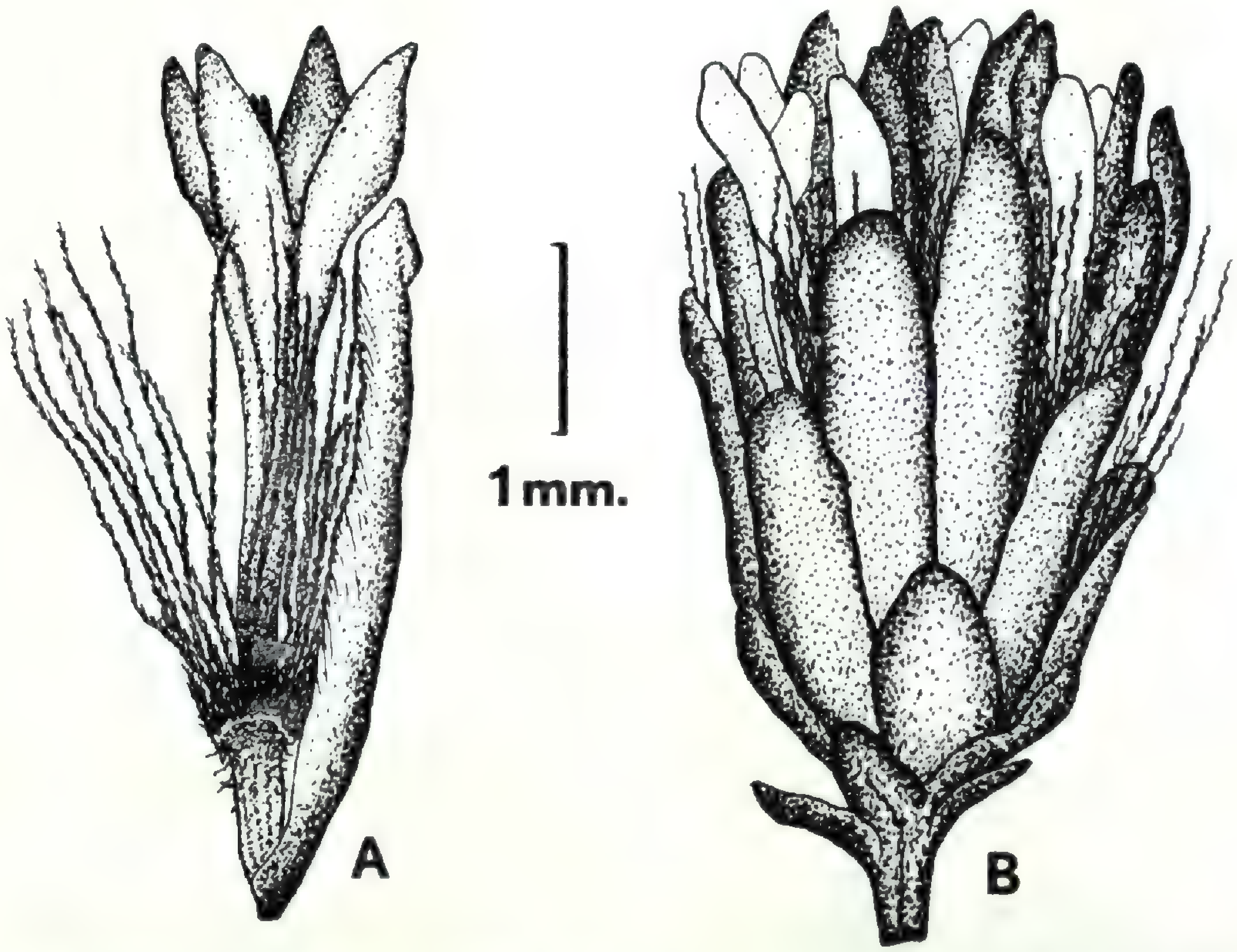

Figure 1. *Solidago juncea* Ait. A — Dissected disk flower with chaff clasping the base of the achene. B — Young head with the chaff protruding through and above the flowers.

Selected voucher specimens supporting this study are the following from the University of Tennessee Herbarium. ONTARIO: Bruce Peninsula, *R. V. Krotkov 9540.* MAINE: Knox Co., *Ray C. Friesner 6182.* NEW HAMPSHIRE: Cheshire Co., *Foster Batchelder.* MASSACHUSETTS: Norfolk Co., *Robert A. Ware 3195.* NEW YORK: Albany Co., *Norman H. Russell n817539.* PENNSYLVANIA: Butler Co., *Norman H. Russell NR-2700.* MARYLAND: Montgomery Co., *Thos. Kearney, Jr.* VIRGINA: Spotsylvania Co., *H. H. Iltis 2317.* KENTUCKY: Jefferson Co., *Charles R. Gunn J-194.* INDIANA: Knox Co., *Ray C. Friesner*

54,333. ILLINOIS: Kankakee Co., *Alfred C. Koelling 166.* The figures were drawn from my personal material. PENNSYLVANIA: Bucks Co., *G. Morton 892.*

BOTANY DEPARTMENT, THE UNIVERSITY OF TENNESSEE
KNOXVILLE 37916

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THE STATUS OF HEDYOTIS PROCUMBENS VAR. HIRSUTA (RUBIACEAE)

ROBERT L. WILBUR[1]

The species *Hedyotis procumbens* (Walt. ex Gmel.) Fosberg (*Houstonia procumbens* (Gmel.) Standley or *Houstonia rotundifolia* Michx.) is a low, creeping somewhat fleshy, heterostylous, perennial herb found along the outer coastal plain from South Carolina south throughout most of peninsular Florida and as far west as eastern Louisiana. It would be noteworthy indeed if any reasonably wide-ranging taxon were found to be completely uniform and this little herb is not in this regard exceptional. For example the leaves vary from narrowly oblanceolate or spatulate to broadly suborbicular but as far as is known differences in neither geography nor ecology are correlated with this morphological variation. Another conspicuous morphologic variable is in vestiture since individuals are either glabrous or very nearly so to so densely hirsutulous as to appear noticeably shaggy upon close inspection. This variation in pubescence has been pointed

[1]Work on this paper was carried out with the support of the National Science Foundation Grant G-18799 and the Duke University Research Council. I should also like to express my appreciation to the curators of the herbaria indicated below by their formulae whose specimens formed the basis of this study: DUKE, FLAS, FSU, GA, GH, MO, NA, NCU, NSC, NY, PH, SMU, US.

out in the formal descriptions of the species since at least Asa Gray's Synoptical Flora (Syn. Fl. 1 (2): 25. 1884) and has been duly noted in such standard references as Small's two major southeastern floristic works (Fl. Se. U.S. 1108. 1903 and Man. Se. Fl. 1255. 1933) and Standley's treatment (N. Am. Fl. 32: 26. 1918).

Recently Lewis (Ann. Mo. Bot. Gard. 53: 377, 378. 1966) typified this species by designating a glabrous specimen as its neotype since the original material has not been found and pubescent plants have not yet been collected in South Carolina. Thomas Walter, the South Carolina planter in whose book this species was first described, stated in the preface to his classic *Flora Caroliniana* that the specimens included came from an area within approximately fifty miles of his plantation on the Santee River. This is located in what is now Berkeley County, South Carolina. Many of the species included, however, must have been obtained during the travels "amounting in the whole to four thousand miles" of his friend, John Fraser, who took Walter's manuscript back to England and oversaw its publication in 1788. In fact, Fraser (Hist. Agrostis cornucopiae . . . p. 4. 1789) stated that his own collections had increased the number of Walter's descriptions from six hundred and forty to one thousand and sixty. There is certainly no evidence for concluding as Lewis has done that Fraser's additions to the Flora largely came from the vicinity of Charleston, South Carolina, or even specifically that *H. procumbens* was apparently collected there. Still, if authentic material of neither Walter nor Fraser is extant, it is perhaps reasonable to choose as neotype a specimen which was collected in the vicinity of Walter's home. If so, it seems a justifiable suspicion that the description in Walter's Flora was based upon the glabrate element since it is known from two counties adjacent to Berkeley County. Hirsutulous specimens have not been seen from South Carolina although they are known from two of the Georgian counties separated from South Carolina only by the Savannah River.

Lewis proposed designating those plants possessing both pubescent upper leaf surfaces and capsules as var. *hirsuta* although noting that var. *procumbens* is occasionally slightly hirsute especially [on its] leaf margins and young leaves." In evaluating the taxonomic merit of the proposed variety, one should note that four of the seventeen specimens cited by Lewis as "representative" of the hirsute variety admittedly also bore material of var. *procumbens*. This woud indicate that there is neither the geographic nor apparently the ecologic separation between the proposed varieties that would be expectd by many taxonomists for a taxon of such a rank. No other isolating mechanism has been suggested.

Specimens of this species from thirteen herbaria have been recently examined by me in an attempt to evaluate the proposed varieties. Doubtless there are more sophisticated and perhaps more convincing ways to evaluate the biological basis of two taxa than by examining hundreds of herbarium specimens. However, I believe that the evidence obtained demonstrates conclusively that the glabrous and hirsutulous plants neither represent biological populations nor are they the type of variation recognized as "varieties" by the majority of American botanists who still employ that category.

Examination of these specimens, I believe, demonstrated the following:

1) No other morphological differences were noted correlated with the variation in pubescence.

2) The majority of the specimens were clearly either glabrous or hirsutulous but a small number of specimens were very sparingly hirsutulous and these naturally prove difficult to assign to either of the proposed varieties.

3) The accompanying maps (fig. 1 and 2) present the distribution of the two pubescence types and shows them to be in large part sympatric.

4) Habitat information on the labels does not suggest ecologic separation between the two pubescence types and,

as was suggested by Lewis' citation of mixed specimens, the two occasionally grow together in the same colony.

There is certainly nothing to indicate from the above that the proposed varieties of *H. procumbens* represent biologically significant populations. There is a greater probability that these pubescence types are variants with as little populational significance as color forms of flowers. Fortunately plants with albino flowers and the like are much less frequently described as taxa with the rank of *formae* today than they were two or three decades ago. The biological significance of such variation is certainly slight and there would seem to be no justification to encumber taxonomy with their formal descriptions and nomenclature. There is certainly not the slightest evidence that the glabrate and hirsutulous plants of this species of *Hedyotis* are members of different breeding populations. It would seem questionable whether taxonomists should continue naming minor genetical variants such as the pubescent phase of *H. procumbens.*

Even though there is a certain logical appeal to recognizing degrees of infraspecific variability by employing a hierarchy of infraspecific categories, not all taxonomists are convinced that this practice is in accord with the biological nature of species or, even if it were, could be objectively applied. Taxonomists perhaps would agree to the desirability of recognized infraspecific categories conveying some approximation of the significance of the nature of the named populations. Unfortunately this is not presently possible for to some investigators the *varietas* is the major infraspecific taxon and for others it is no more than a biologically insignificant abberation of the sort that has been designated *forma* if named at all. Consequently one must now reinvestigate each new proposal to understand the nature of the variation in order to determine how its author employs a given unit of the taxonomic hierarchy. This lack of precision and uniformity in usage is unscientific and certainly self-defeating.

Those botanists who have adopted subspecies as a substi-

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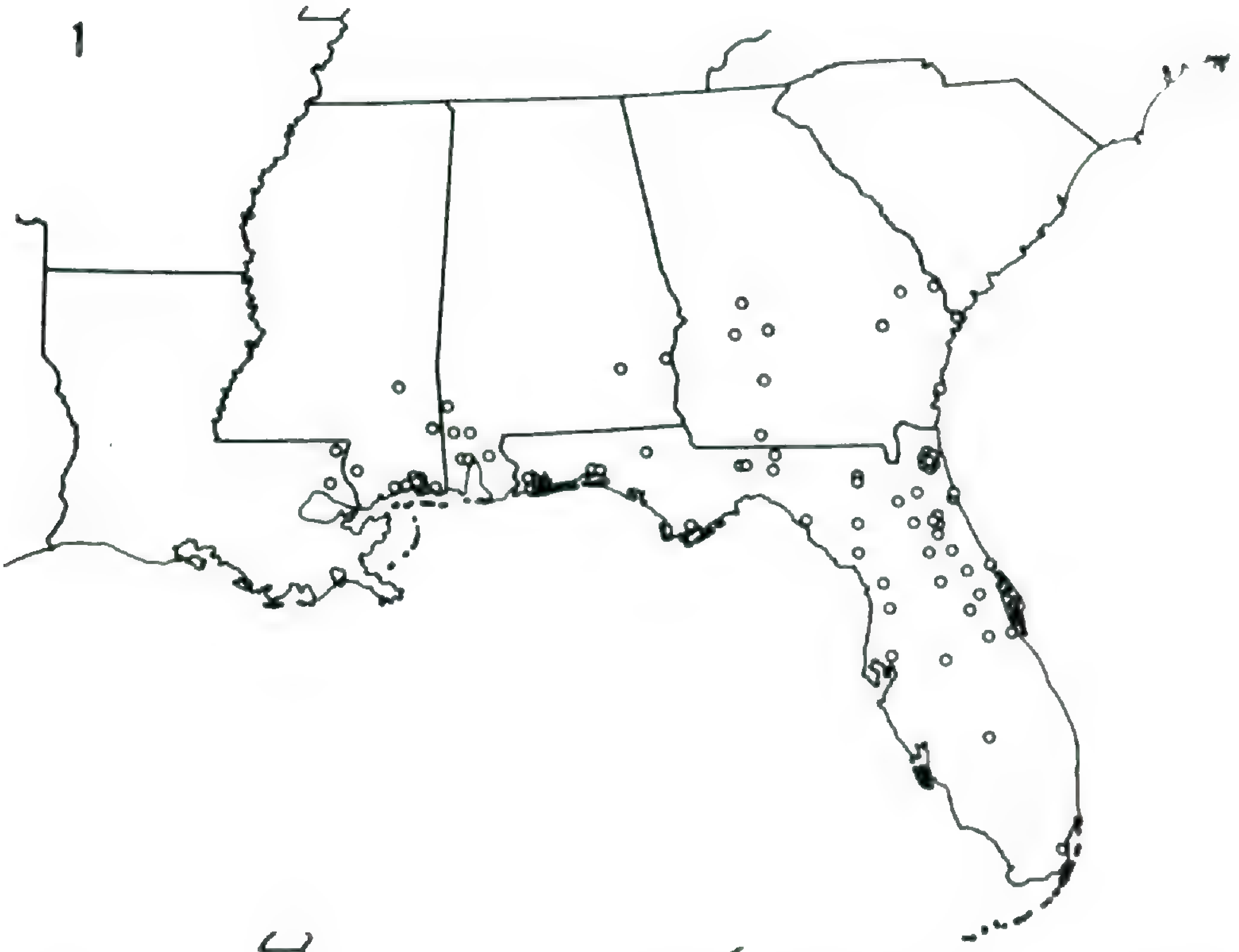

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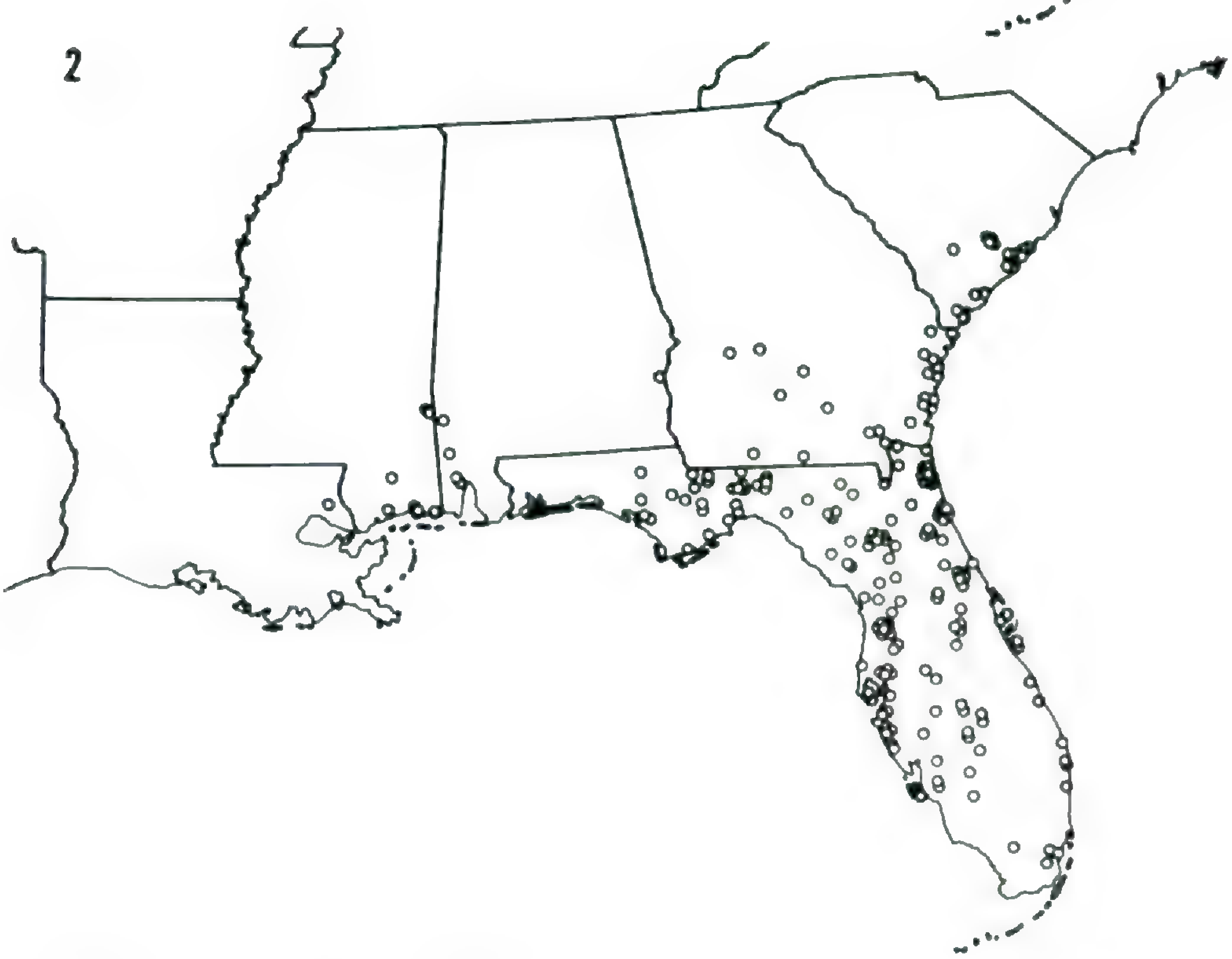

Maps 1-2. Map 1. Distribution of hirsutulous specimens of *Hedyotis procumbens*. Map 2. Distribution of glabrate specimens of *Hedyotis procumbens*.

tute for variety for geographically and/or ecologically separated populations in an effort to conform their own usage to that of the zoologists might read with profit the long series of articles appearing in Systematic Zoology and other journals in the last decade or so in order to see how little unanimity actually exists within zoology as to the proper application of the category "subspecies."

Although the International Code of Botanical Nomenclature wisely refrains from arbitrarily defining the various infraspecific categories, it is most unfortunate that there is so little uniformity in usage especially now that taxonomists are set to embark jointly upon some very ambitious floristic endeavors. Perhaps half of the American taxonomists now use subspecies in the same sense that the remainder use variety *i.e* for morphologically distinctive populations occupying discrete geographic areas or different major ecological sites. Certainly further effort should be made to resolve this confusing difference in practice before major floras appear reflecting in the diverse infraspecific categories employed not so much the difference in our knowledge of the biology of the taxa but the personal bias of the contributor of a given family or genus.

DEPARTMENT OF BOTANY, DUKE UNIVERSITY
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SOME IMPACTS OF SPRUCE'S AMAZON EXPLORATIONS ON MODERN PHYTOCHEMICAL RESEARCH*

RICHARD EVANS SCHULTES

It was on July 12, 1849 that one of the most extraordinary feats of botanical exploration in South America began. For, on that day, Richard Spruce arrived at Belém do Pará to start his epoch-making phytogeographic studies and collections in the Amazon Valley and the northern Andes from 1849 to 1864 (15, 23).

Undoubtedly one of the greatest explorers of all times, his name is known today to a mere handful of people whose interests in botany and travel have inevitably brought them face to face with the life and work of this great man.

Richard Spruce was born in the tiny hamlet of Ganthrope, a few miles from Malton, Yorkshire, on September 10, 1817, and died seventy-six years later in the neighboring hamlet of Coneysthrope, on December 28, 1893. The simplicity of his life is admirably brought out by this one fact: having travelled for fourteen years the wildest of areas — some so inaccessible that only now, after the passage of one hundred years, are scientists again penetrating them — Spruce returned, not to London or permanently to any of the great botanical centres of Britain, but to a little cottage in his native countryside. For it was his childhood rambles in this fascinating countryside that had fostered

*Presented by invitation at the III International Pharmacological Congress, São Paulo, Brazil, July 24-30, 1966.

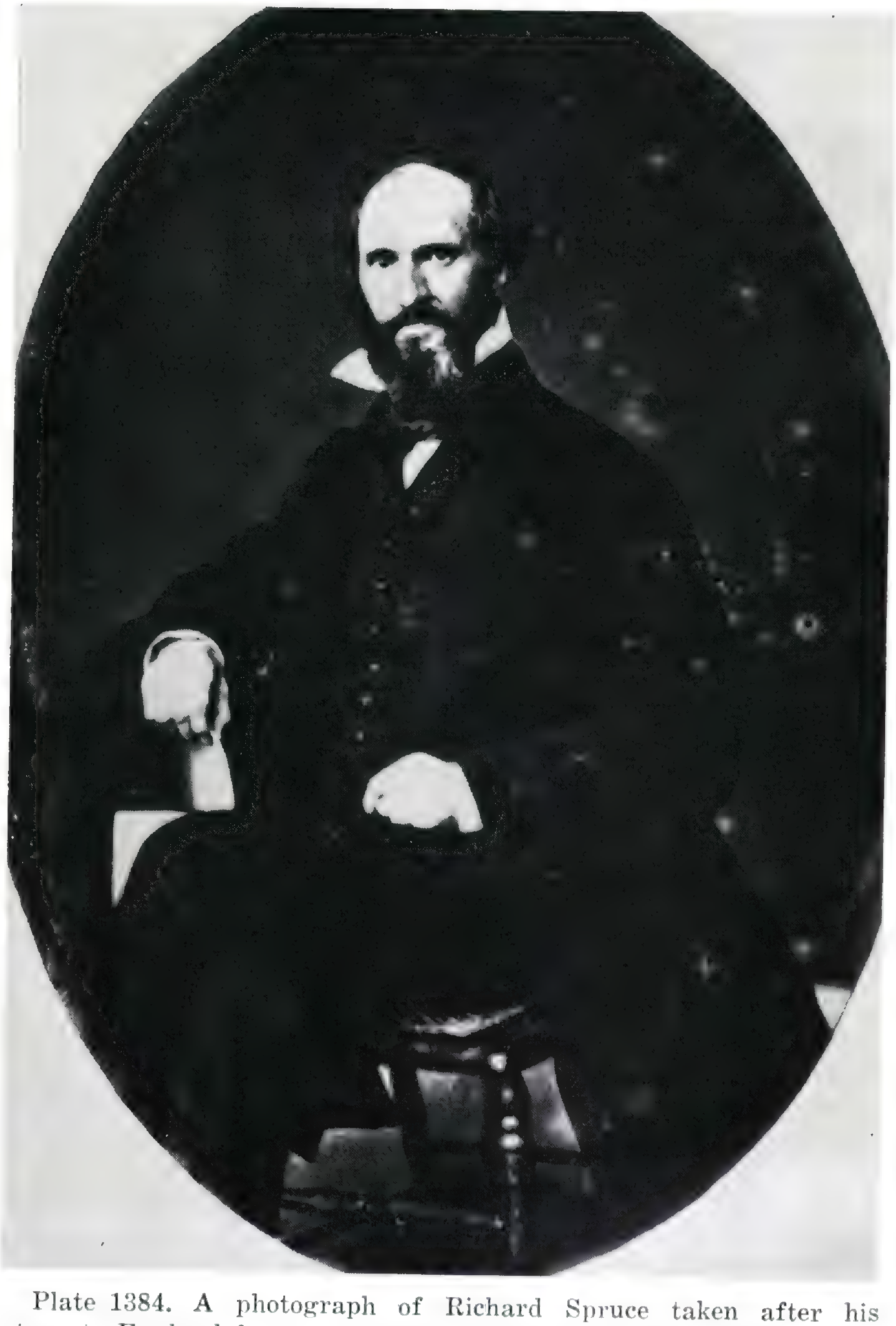


Plate 1384. A photograph of Richard Spruce taken after his return to England from his South American expeditions. Original in the Gray Herbarium of Harvard University.

his love and knowledge of botany which developed at such an early period of his life that, in his sixteenth year, he had compiled a list of 403 species of plants of Ganthrope, followed, several years later, by a List of the Flora of the Malton District, enumerating 485 species. It was during this period that he became deeply absorbed in mosses and liverworts, "the joy of his early manhood and the consolation of his declining years," groups of plants in which he became an investigator whose authority will stand as long as men delve into the natural history of the bryophytes.

In Spruce, we find perhaps the greatest contrasts ever known in a botanist. A man of extremely delicate health and plagued by chronic ills, he betook himself to one of the wildest and least known jungle areas of the world, to spend fourteen years of his life in hard physical work, constant exposure to the tropical elements and diseases, insufficient diet, and complete lack of even rudimentary comforts. A scholar with a thorough classical training and of outstanding cultural and scientific attainments, he divorced himself from all centres of culture and lived for long periods amongst Indians or unlettered half-breeds. A superb correspondent, he plunged himself into regions where, for months on end, he received not one letter or newspaper. A botanist whose training and first love concerned mosses and hepatics — the most diminutive of land plants — he carried out painstaking research on some of the most gigantic of tropical trees and lianas, even discovering hundreds which had hitherto been unknown to science. A poor man, he contributed through his work on the quinine-tree in Ecuador, to the creation of great plantations and fortunes, which resulted from the domestication of this plant in the British possessions of the Far East. A mild-mannered and dignified person, he feared none of the dangers that his expeditions presented, and more than once had to take measures to defend his very life. A student whose scientific training had fitted him to handle masses of minute detail, he was able to cope with the endless problems attendant on the organisation and execution

of cumbersome trips by canoe or on horseback of months' or even years' duration. And, perhaps most astonishing of all: a naturalist who looked with abhorrence on the philosophy that nothing not immediately beneficial to man was worthy of study, he nevertheless provided science with the first extensive botanical knowledge of Hevea rubber (which was just then beginning to attract extensive commercial attention), made far-reaching practical researches on the quinine-tree and filled his note-books with observations and studies on all manner of native economic plants, including gums and resins, fibres, foods, drugs, narcotics and stimulants, oils, dyes, and timbers.

But what has this mild-mannered botanical explorer of a century ago to do with a modern phytochemical survey of the Amazon? When answering this question, we might find it somewhat paradoxical to read from one of Spruce's letters the following philosophy. Speaking of his special group, the liverworts, he wrote: "I like to look upon plants as sentient beings, which live and enjoy their lives — . . . when they are beaten to pulp or powder in the apothecary's mortar, they lose most of their interest for me. It is true that the *Hepaticae* have hardly as yet yielded any substance to man capable of stupefying him or of forcing his stomach to empty its contents, nor are they good for food; but if man cannot torture them to his uses or abuses, they are infinitely useful where God has placed them, as I hope to live to show; and they are, at the least, useful to and beautiful in themselves — surely the primary motive for every individual existence." Are these, you may justifiably ask, sentiments conducive to research into drug plants? Strangely enough, I would answer you a very definite *yes*, for they bespeak the deepest love for plants which, after all, must underlie any success in our search for promising new physiologically active substances through ethnobotany.

Spruce lived closely with the native Amazonian peoples, seldom interrupting his stay with trips to urban centres. He learned several of their languages. He had an ever inquisitive mind and a most perceptive botanical eye. For

a number of plants that have later attracted extensive phytochemical and medical attention — and which are still claiming serious study — it was Spruce who gave us detailed, accurate and pioneer information.

A very thorough study of this field information might serve modern phytochemistry well in orienting the search for new physiologically active plants or in investigating more deeply and critically those which we do know. In this discussion, I have chosen to speak about Richard Spruce, but I might have talked about any of a dozen of the earlier botanical explorers of tropical America. Most of them — Humboldt, Schomburgk, Martius and others — are repositories of such information, in great part neglected or not fully exploited by the modern phytochemist. Do I dare to hope that the following words will help turn us back to these rich notes of dedicated field men, most of whom jotted down their notes fired merely by academic curiosity, not by commercial interest? If we do give their writings some consideration, there is always the possibility that, at the moment least expected, we might be led into discoveries of unprecedented potentialities.

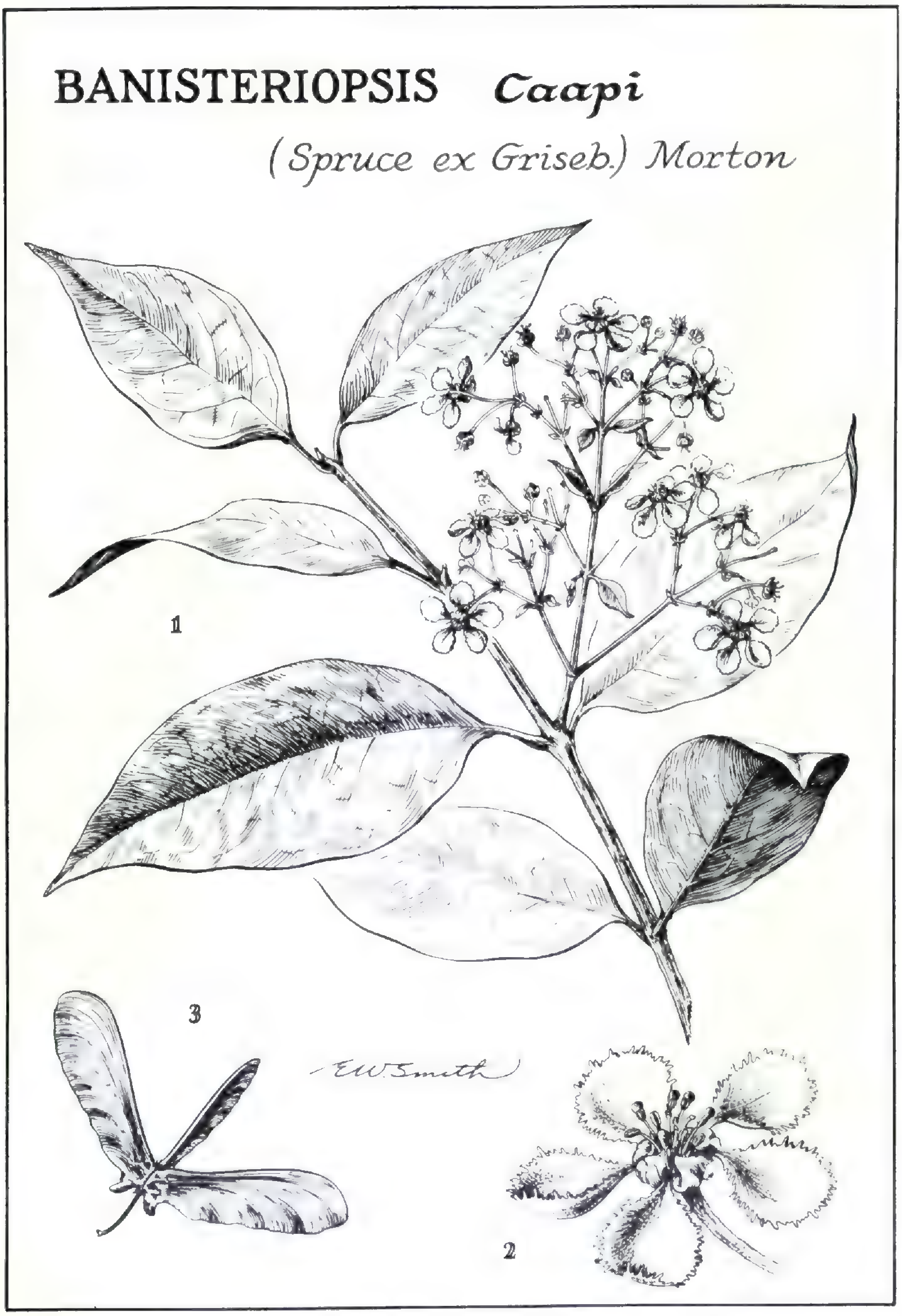
Of the numerous narcotic preparations used by witch-doctors in religious, curative and magic rites in South America, Spruce was an early student of two. "Having had the good fortune," he wrote, "to see the two most famous narcotics in use and to obtain specimens of the plants that afford them sufficiently perfect to be determined botanically, I propose to record my observations on them, made on the spot."

From the point of view of modern phytochemistry, however, it is undoubtedly Spruce's pioneer work on the malpighiaceous narcotics of South America that commands prime attention. One hundred and fourteen years have passed since the botanical identification of the principal species involved. In the intervening century, an appreciable amount of botanical and ethnobotanical research has been devoted to these interesting hallucinogens. Notwithstanding this long period of accomplishment, we find it necessary

— even for the proper prosecution of chemical studies today — to study and re-evaluate Spruce's meticulous field observations.

In 1852, during the early stages of his five years of field work on the upper Rio Negro of Brazil and adjacent Colombia and Venezuela, Spruce learned of the use by Tukanoan Indians of the extraordinary drug called *caapi.* It was employed to induce, for prophetic and divinatory purposes, a narcosis characterised, amongst other strange effects, by frighteningly realistic coloured visual hallucinations and a feeling of extreme and reckless bravery. Unlike many of the early reports of similar narcotics, Spruce's contribution included a precise determination of the botanical source of the drug. Finding caapi cultivated along the Rio Negro, he noted that "here were about a dozen well growing plants . . . twining up to the tree tops along the margin of a *roça* [a cultivated plot] and several smaller ones. It was fortunately in flower and young fruit; and I saw, not without surprise, that it belonged to the order Malpighiaceae . . ." A collection in full flower *(Spruce 2712)* was taken from the liana used by the natives in preparing the intoxicating caapi-drink. Spruce drew up a description of the species from living specimens. He allocated the species to the genus *Banisteria*, calling it *Banisteria Caapi.* This description was then published by the botanist Grisebach. As taxonomic knowledge of the Malpighiaceae became more refined in the present century, the American specialist Morton ascertained that this species-concept could not with precision be included in *Banisteria* and, in 1931, he transferred it to a new but closely allied genus that he characterized and named *Banisteriopsis* (9). The caapi liana is, accordingly, now correctly called *Banisteriopsis Caapi* (Spr. ex Griseb.) Morton.

Spruce's observations were recorded in his wonted preciseness in 1852. About 1870, back in England, he wrote an article on the narcotic caapi and published it in a very obscure journal. This account was included as a special chapter in Wallace's posthumous account of Spruce's travels


BANISTERIOPSIS Caapi
(Spruce ex Griseb.) Morton
1
3
2
E.W. Smith

and work in 1908: "A botanist on the Amazon and Andes". In publishing almost intact Spruce's account, Wallace observed very truthfully that "the whole essay affords a good example of the writer's style and of his power of making even technical details interesting and of introducing bright descriptive flashes and touches of human nature in what might otherwise be a rather dry exposition of botanical and pharmaceutical facts."

Spruce, though a brave and daring explorer, unfortunately was a very sick man. This is probably the explanation of his hesitation fully to experiment personally with caapi — most regrettably so because notes on the effects of the intoxicant from such an analytical mind would have been of extreme value to modern investigators. "I had gone [to a caapi-drinking Indian festival] with the full intention of experimenting the caapi on myself, but I had scarcely dispatched one cup of the nauseous beverage, which is but half a dose, when the ruler of the feast — desirous, apparently, that I should taste all his delicacies at once — came up with a woman bearing a large calabash of *caxiri* (mandiocca beer), of which I must needs take a copious draught, and as I know the mode of its preparation, it was gulped down with secret loathing. Scarcely had I accomplished this feat, when a large cigar, 2 feet long and as thick as the wrist, was put lighted into my hand, and etiquette demanded that I should take a few whiffs of it — *I* who had never in my life smoked a cigar or a pipe of tobacco. Above all this, I must drink a large cup of palm wine, and it will readily be understood that the effect of such a complex dose was a strong inclination to vomit, which was only overcome by lying down in a hammock and drinking a cup of coffee . . ."

In those years, explorers rarely gathered material for phytochemical analysis, and in Spruce's case the great distance and isolation of this scene of field work and the primitiveness and absence of normal communications one might think would have made it impracticable or impossible for him to gather material in bulk for pharmaceutical spe-

cialists. In spite of these drawbacks, however, we know that Spruce did try so to enrich science but, like so many explorers even in modern days, was frustrated in his attempt. "I obtained a good many pieces of stem, dried them carefully, and packed them in a large box, which contained botanical specimens, and dispatched them down the river for England in March 1853. The man who took that box and four others on freight, in a large new boat he had built on the Uaupés, was seized for debt when about half-way down the Rio Negro, and his boat and all its contents confiscated. My boxes were thrown aside in a hut, with only the damp earth for floor, and remained there many months, when my friend Senhor Henrique Antonij of Manáos . . . succeeded in redeeming them and getting them sent on to the port of Pará. When Mr. Bentham came to open them in England, he found the contents somewhat injured by damp and mould, and the sheets of specimens near the bottom of the boxes quite ruined. The bundle of caapi would presumably have quite lost its virtue from the same cause, and I do not know that it was ever analysed chemically; but some portion of it should be in the Kew Museum at this day."

One of the most interesting exercises that I can imagine would be the analysis of a small portion of this original Spruce material — if, indeed, it is still preserved at Kew — with our modern improved chemical techniques. The active priciples of caapi (harmine type alkaloids) might not have deteriorated with the mildew, and it is possible that even in this more than a century of storage the alkaloids would be intact.

Proof that, even a century ago, Spruce's thinking was, at least in part, along chemotaxonomical directions may be seen when, upon determining caapi as a new species of Malpighiaceae, he mused: "My surprise arose from the fact that there was no narcotic malpighiad on record, nor indeed any species of that order with strong medicinal properties of any kind. *Byrsonima* — a malpighiaceous genus that abounds in the Amazon Valley — includes many spe-

cies . . . Their bark abounds in tannin and is the usual material for tanning leather at Pará, as also, by the Indians, for dyeing coarse cotton garments a red-brown colour. Another genus — *Bunchosia* — grows chiefly on the slopes of the Andes . . . the seed is described in books as poisonous, and if it be really so, then it is the only instance, so far as I know, of the existence of any hurtful principle in the entire family . . . excepting . . . the caapi." "Yet," he prophetically and very correctly remarked, "strong poisons may lurk undiscovered in many others of the order, which is very large and (the twining species especially) of great sameness of aspect; and the closely allied Soapworts (Sapindaceae) contain strong narcotic poisons, especially in the genus *Paullinia*."

The second time that Spruce met with caapi was in June 1854 at an encampment of the wholly uncivilised Guahibo Indians along the Orinoco at the cataracts of Maypures. The Guahibos not only prepared caapi, like their neighbours where Spruce had first seen the drug, as an intoxicating drink, but they "chew the dried stem, as some people do tobacco." Spruce learned from these roving peoples that "all the native dwellers on the rivers Meta, Vichada, Guaviare, Sipapo and the intervening smaller rivers [in Colombia and Venezuela] possess caapi and use it in precisely the same way."

Again, in 1859, whilst working in the Ecuadorian Andes, he encountered the Zaparo Indians using a narcotic that they called *ayahuasca*. Spruce wrote that he "again saw caapi planted" in this area and that "it was the identical species of the Uaupés, but under a different name, in the language of the Incas, *aya — huasca*, i.e. "dead man's vine."

Spruce reported that years earlier, Dr. Manuel Villavicencio had recorded in his *Geografía de la República del Ecuador* that the sundry tribes of the upper Río Napo in Amazonian Ecuador employ ayahuasca for sorcery, witchcraft, prophecy and divination. Although apparently no specimens were taken and no reference to botanical identification was made in Villavicencio's account, that included

a report on self-intoxication, the common name *ayahuasca* was used and the source plant was described as a liana. All later work has shown that ayahuasca in Ecuador and Peru refers to *Banisteriopsis*. Indeed, as Spruce noted, although "of the plant itself," Villavicencio "could tell no more than that it was a liana or vine," his "account of its properties" coincided "wonderfully with what I had previously learnt in Brazil."

All subsequent serious botanical workers on caapi and ayahuasca have substantiated Spruce's very astute judgment — that the two names refer to essentially the same narcotic drink made from *Banisteriopsis*. Recent field work has uncovered the possibility that other species than *Banisteriopsis Caapi* are used: *B. inebrians*, *B. quitense*, *B. Rusbyana*, for example. Still there is not yet agreement amongst modern botanists that these are really distinct species, some taxonomists believing that they are merely synonyms of an unusually variable *Banisteriopsis Caapi*. This justifiable and, at our present state of taxonomic knowledge, truly understandable doubt plagues phytochemists almost as much as the several uncertainties and confusions injected into the picture of the malpighiaceous narcotics by hasty, untrustworthy and widely disseminated writings of so-called "experts" in the recent past. From the phytochemist's point of view, a critical study of Spruce's notes will help rectify much of the confusion that reigns at the present time.

In 1905, a Colombian, Rocha, published an account of his trip to the headwaters of the Ríos Caquetá and Putumayo in Amazonian Colombia, reporting that the natives employed as an hallucinogen a "little bush" or "leaves" called *yajé* (12). His account of the properties of yajé coincided strikingly with those described for ayahuasca by many authors, and it was widely assumed that yajé and ayahuasca were identical as to the source plant. German, Russian, Colombian and American botanists who have worked in the Colombian Putumayo have all substantiated this viewpoint — with or without voucher specimens. Yet

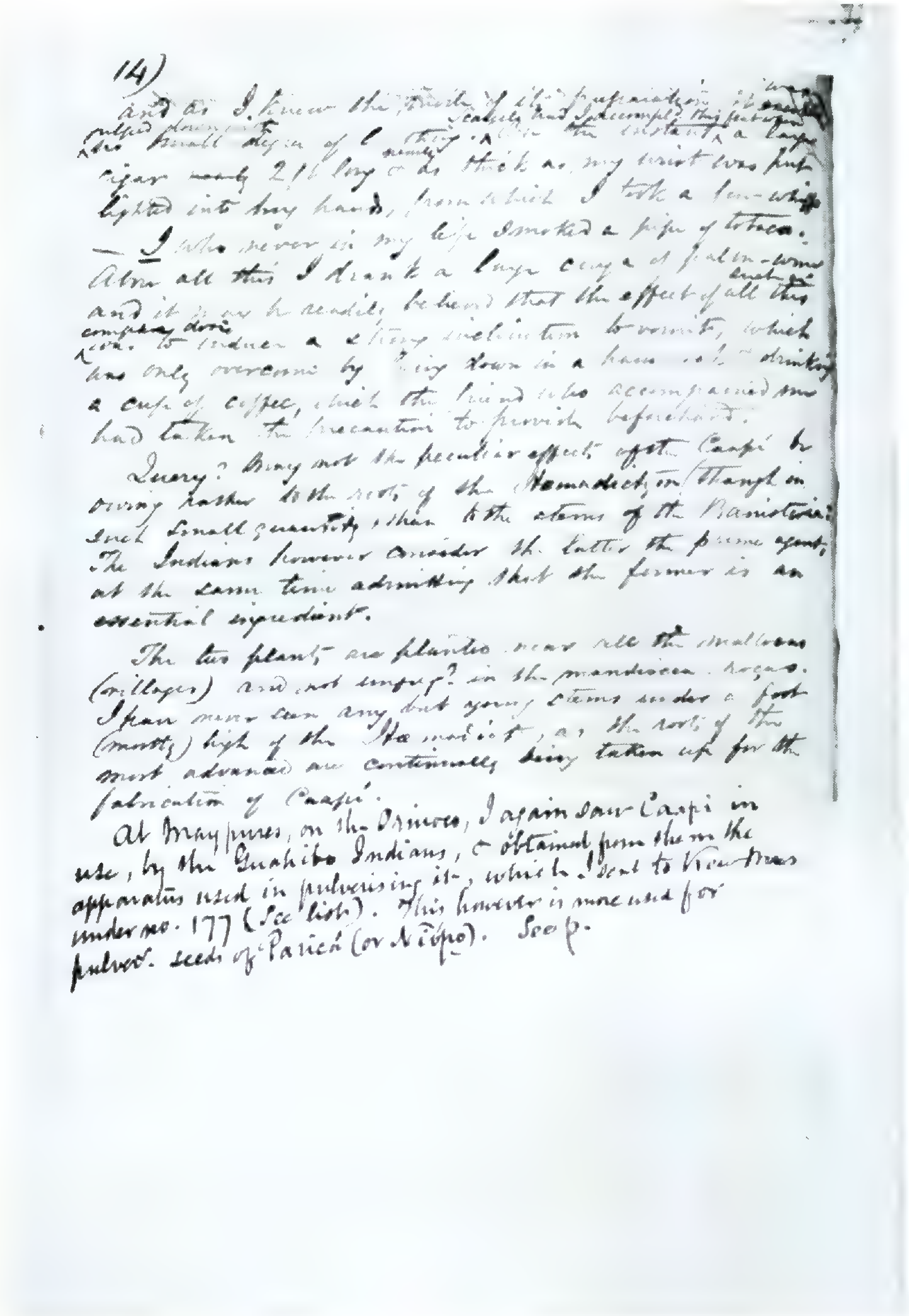
certain anthropological and pharmaceutical writers, mainly French and none of whom have been in the field, have created a state of confusion almost impossible of disentanglement concerning the source of yajé.

This confusion began when Rouhier (13) suggested that yajé could be an *Aristolochia*, a suggested identification that was accepted by the Colombian chemist Fischer (4). It was, however, the French anthropologist Reinberg (10) who first seems adamantly to have asserted that ayahuasca and yajé might be different plants. Reinberg reported that his assertion that ayahuasca and caapi were conspecific but that yajé could be, with reservations, referred to *Prestonia amazonica*, was based on herbarium material, but, in 1950, I made a search of the Paris herbarium and found there no evidence whatsoever of any material supporting such a novel interpretation.

Since then, numerous French and Belgian writers have fallen into line, accepting Reinberg's "identification" of yajé, even though the Belgian pharmacologists, Michaels and Clinquart (8), obviously more conservative than their French anthropological confrères, dismissed as "doubtful" the possibility that yajé could be referable to *Prestonia amazonica*. Other French writers arrived at even more extraordinarily inexplicable conclusions, but more recently Fabre (3), in reviewing the historical aspects of the identification of ayahuasca, caapi and yajé, concluded that all three are prepared basically from *Banisteriopsis*.

All of these confused reports about *Prestonia amazonica* as a narcotic stem from the way the work of Richard Spruce is interpreted. This confusion has so hindered and atrophied phytochemical research that, in 1950, I decided to consult Spruce's field notes preserved at the Royal Botanic Gardens at Kew in England. Would that all who had written on these drugs had had the meticulous scholarship of Richard Spruce!

When Spruce described caapi as a product of the malpighiaceous *Banisteriopsis* [*Banisteria*] *Caapi*, he stated that there was another kind of caapi in the same region and


14) And as I knew the strength of this preparation [illegible] scarcely had I accomplished this feat [illegible] the small dozen of [illegible] the instant a large cigar nearly 2 ft long & as thick as my wrist was put lighted into my hands, from which I took a few whiffs — I who never in my life smoked a pipe of tobacco. Above all this I drank a large cuya of palm-wine and it may be readily believed that the effect of all this [illegible] was to induce a strong inclination to vomit, which was only overcome by lying down in a hammock & drinking a cup of coffee, which the friend who accompanied me had taken the precaution to provide beforehand.

Query? May not the peculiar effects of the Caapi be owing rather to the roots of the Haemadictyon (though in such small quantity) than to the stems of the Banisteria? The Indians however consider the latter the prime agent, at the same time admitting that the former is an essential ingredient.

The two plants are planted near all the malocas (villages) and not unfreq? in the mandiocca rogas. I have never seen any but young stems under a foot (mostly) high of the Haemadictyon, as the roots of the most advanced are continually being taken up for the fabrication of Caapi.

At Maypures, on the Orinoco, I again saw Caapi in use, by the Guahibo Indians, & obtained from them the apparatus used in pulverising it, which I sent to Kew Museum under no. 177 (See list). This however is more used for pulverd. seeds of Parica (or Niopo). See p.

Plate 1385. A page from Spruce's field notebook describing the possibility that *Haemadictyon* might be added occasionally to the caapi drink made from *Banisteriopsis Caapi*. Courtesy of the Royal Botanic Gardens, Kew, England.

that it was called *caapi-pinima* or "painted caapi." In his field notebook, preserved at Kew, he wrote: "2712 *Banisteria Caapi* Mss. From this is prepared an intoxicating drink known to all the natives of the Uaupés by the name of caapi. The lower part of the stem, which is the thickness of the thumb swollen at the joints, is the part used. This is beaten in a mortar with the addition of water and a small quantity of the slender roots of the *Apocynac.* (Apparently a *Haemadictyon*) called caapi-pinima or painted caapi, from its leaves being stained and veined with red . . . Query? May not the peculiar effects of the caapi be owing rather to the roots of the *Haemadictyon* (though in such small quantity) than to the stems of the *Banisteria*? The Indians, however, consider the latter the prime agent, at the same time admitting that the former is an essential ingredient. The two plants are planted near all mallocas (villages) . . ."

When these notes were published in 1908, they suffered a slight, but significant, change of emphasis. The terms of qualification disappeared. The published version states that caapi-pinima "is an apocynaceous twiner of the genus *Haemadictyon*, of which I saw only young shoots, without any flowers. The leaves are of a shining green, painted with the strong blood-red veins. It is possibly the same species . . . distributed by Mr. Bentham under the name *Haemadictyon amazonicum* n.sp. It may be the caapi-pinima which gives its nauseous taste to the caapi . . . and it is probably poisonous, . . . but it is not essential to the narcotic effect of the *Banisteria*, which (so far as I could make out) is used without any admixture by the Guahibos, Zaparos and other nations out of the Uaupés."

Spruce was one of South America's most meticulous of scientific observers. A less careful and botanically untrained observer might easily have confounded the young shoots of *Haemadictyon amazonicum* (now correctly called *Prestonia amazonica*) with *Banisteriopsis*, for the leaves of both are opposite, and the leaves of some species of *Prestonia* do resemble remarkably those of *Banisteriopsis* in shape and texture. But Spruce could never have confused

an apocyaceous plant, full of a white latex, with a *Banisteriopsis*. He might have erred as to genus, for the genera of the Apocynaceae are often hard to distinguish even with flowers. But even this possibility would seem, in the case of Spruce, to be remote. In my own many years of exploration in the Rio Negro basin of Colombia and Brazil, I followed along Spruce's itinerary in great part and searched especially for an apocynaceous vine growing around Indian huts, as described by Spruce: although every Indian *Manihot*-plot boasts its several cultivated vines of *Banisteriopsis*, nothing resembling a *Prestonia* was ever seen under cultivation.

A careful reading of Spruce's notes reveals that he never claimed more for *Prestonia* or caapi-pinima than the role of an admixture. We know from reports of later investigators that other plants are sometimes added in small amounts to the beverage prepared from *Banisteriopsis*, in the belief that they change or fortify the effects of the narcotic drink. For example, I (18) reported the admixture of leaves of an apocynaceous tree — possibly *Malouetia Tamaquarina* — by the Makunas of the Río Popeyacá of Colombia. Later writers, without supporting herbarium specimens and taking their cue from Spruce whose notes and files they misread or misunderstood, now propose that the narcotic drink in one part of the Amazon, where it is known as yajé, is prepared exclusively from *Prestonia amazonica*. For this assertion, there is absolutely no basis in field work.

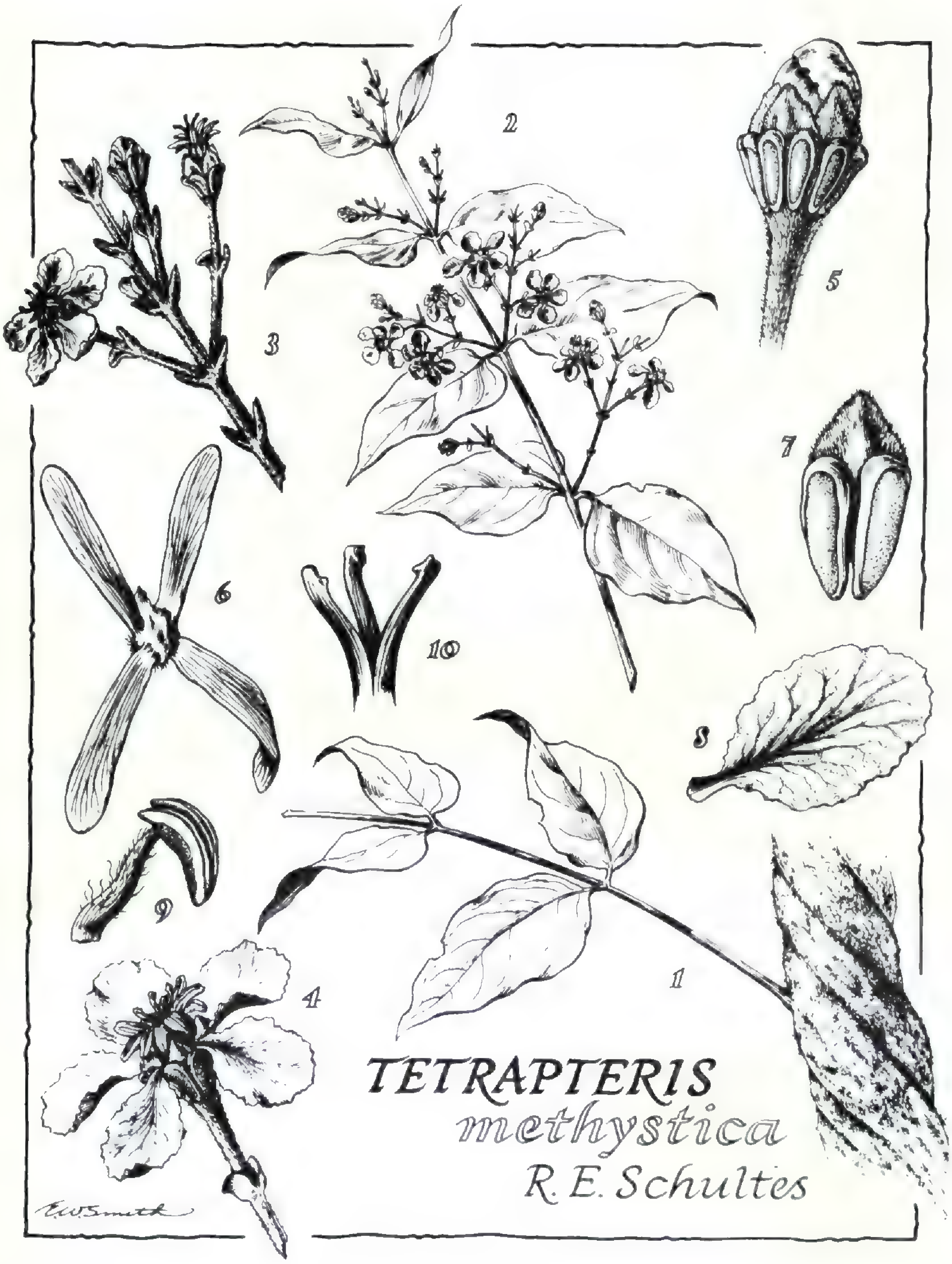
Prestonia amazonica is known, furthermore, from only one collection — the type collection made by Spruce in 1859 at Trombetas on the lower Amazon. In more than a century, the species has never been found again. We are forced to conclude, consequently, that *Prestonia amazonica* is either a very rare species or else a strict endemic, confined to the general region of the type collection. The Rio Trombetas lies more than 1200 miles in a straight line from the eastern slopes of the Andes of Colombia, where we are expected to believe that the natives are using this rare species in rela-

tive abundance as the source of their frequently employed yajé.

The chances that *Prestonia amazonica* is used are, for all practical purposes, non-existent; and there seems to be no evidence that any species of *Prestonia* is so employed along the eastern slopes of the Andes of Colombia and Ecuador — or indeed in the entire Amazon. Even in the area where Spruce reported its possible use a hundred years ago, there is all probability that, if employed at all, it was utilized solely as an admixture with *Banisteriopsis*. Nevertheless, modern phytochemistry would do well to investigate this reportedly poisonous apocynaceous genus of some 30 species of tropical America. Little is known of *Prestonia* chemically, and the recently published analysis of *P. amazonica*, in which the presence of N — N dimethyltryptamine was reported, was undoubtedly based on a misidentified infusion made from *Banisteriopsis Caapi* (22).**

Spruce reported that the Indians of the Rio Uaupés distinguished two kinds of caapi, the minor one called *caapi-pinima*. Much later, Koch-Grünberg (7) found that the Tukanos of the Uaupés know two kinds, but he could identify botanically only one: *Banisteriopsis Caapi*. In 1948, one hundred years after Spruce, I discovered the Indians on the Rio Tikié, a Brazilian affluent of the Uaupés, preparing an intoxicating drink from the malpighiaceous genus

**Very recently, one of my graduate students, Mr. Homer V. Pinkley, learned that the Kofán Indians of Amazonian Ecuador sometimes add the leaves of *Banisteriopsis Rusbyana* to the drink prepared from the bark of *B. Caapi* or *B. inebrians* to "fortify" it. Holmstedt (in litt.) informs me that an analysis of these leaves collected by Pinkley indicates that the species contains harman alkaloids and N, N-dimethyltryptamine. *Banisteriopsis Rusbyana* is called *óco-yaje* by the Kofán; *B. Caapi* and *B. inebrians* are known simply as *yaje*, as is the narcotic drink. One is led to wonder, in view of this recent discovery, whether or not the admixture so often stated to be *Prestonia amazonica*, from which the tryptamine was erroneously reported, is, in reality, *Banisteriopsis Rusbyana*. The material analysed by Holmstedt has been identified against a voucher collection: *Pinkley 449*, deposited in the Economic Herbarium of Oakes Ames in the Botanical Museum of Harvard University. (R. E. S. July, 1968).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TETRAPTERIS
methystica
R. E. Schultes
E.W. Smith

Tetrapteris: from a species called *T. methystica* (16). From the bark of this gigantic forest liana, with no admixtures, a bitter beverage is prepared. I experimentally learned that it had strong hallucinogenic properties. The drink was rather yellowish, unlike the usual chocolate-brown of the drink prepared from *Banisteriopsis Caapi*. One wonders whether or not the term "painted caapi" reported by Spruce could have referred to the kind of caapi that makes this unusual yellowish drink.

The confusion resulting from the misinterpretation, misrepresentation and misunderstanding of Spruce's very obvious suggestions concerning *Prestonia* as a possible narcotic are, unfortunately, typical of so much that plagues modern phytochemistry and that will continue to do so, until more thorough botanical evidence is demanded by non-botanical writers before categoric statements are made either on carefully qualified suggestions or without voucher specimens.

A century of research work, from Spruce's time to the present, has given us an appreciable body of information about ayahuasca, caapi and yajé, but much still remains to clarify and much still remains to discover. There are numerous problems demanding research, problems not even touched upon by Spruce. One of these concerns the use of admixtures with *Banisteriopsis* and the identity of the plants employed as admixtures. Another concerns different "kinds" of basic plants employed. This problem has been reviewed recently in the literature (5, 18). Most recently, a Brazilian anthropologist, Alves da Silva (1) has indicated, through aboriginal names, the use of five presumably different lianas and several admixtures in the preparation of caapi by the Tukanos in the very region where Spruce's work was done one hundred years ago.

The second hallucinogen that Spruce encountered and studied assiduously in the field was the *yopo* or *niopo* snuff of the upper Orinoco of Colombia and Venezuela.

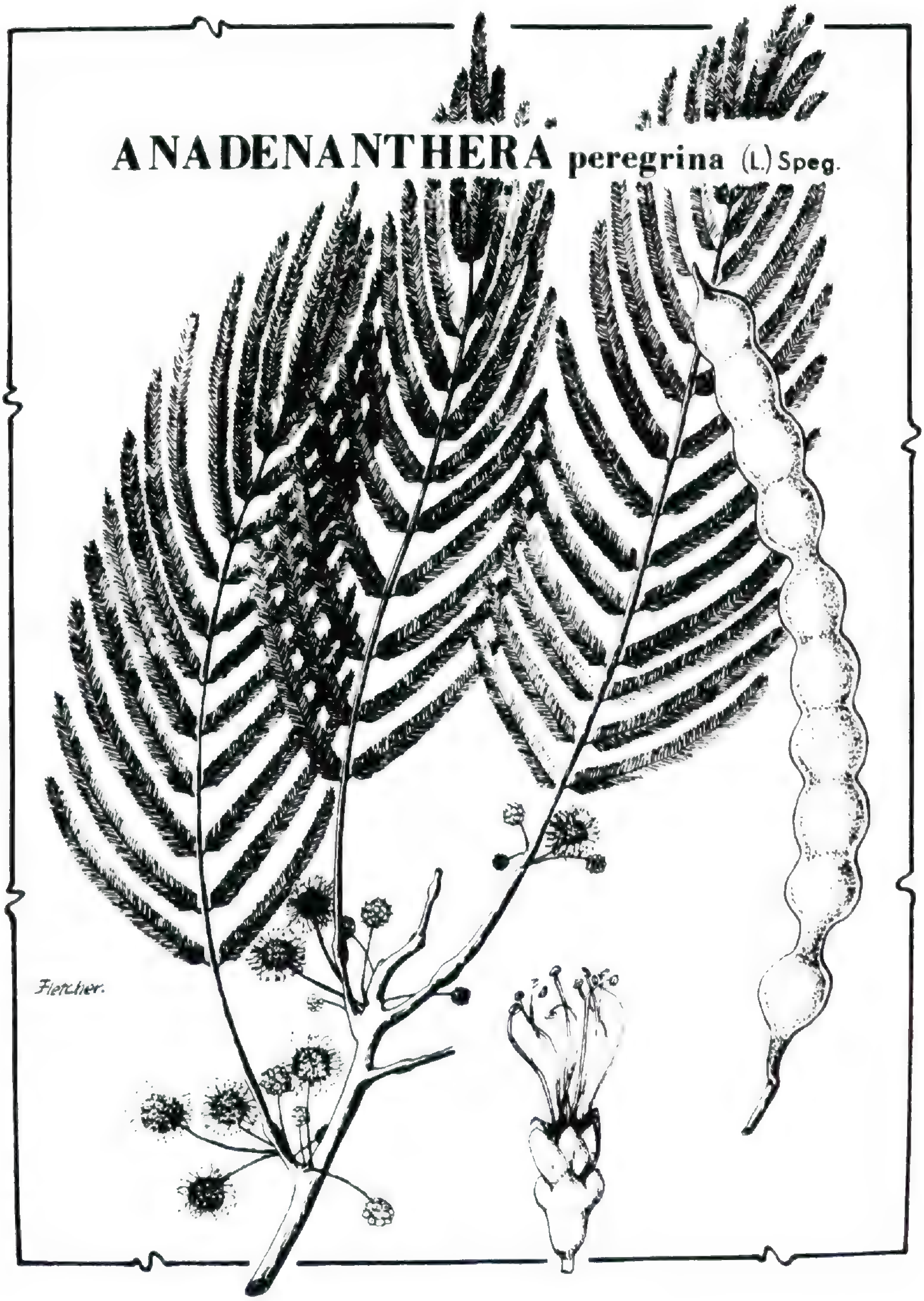
It was Humboldt's expedition that first identified the source plant as a species of the leguminous genus *Pipta-*

denia in 1801 (6). There is a very brief account of its narcotic use: "Ex seminibus tritis calci vivae admixtis fit tabacum nobile que Indi Otomacos et Guajibos utuntur." The plant was first described by Humboldt as a species possibly of *Acacia*: then it was transferred to the genus *Inga*; finally, it was accommodated in *Piptadenia* as *P. Niopo.*

Spruce collected material of the plant *(Spruce 1786)* along the Rio Janauarí. Bentham determined it as Linnaeus' *Mimosa peregrina* but placed it in the genus *Piptadenia,* thus altering its name to *P. peregrina.* This is the name by which the source of yopo snuff has been known until recently, when modern taxonomic studies have tended to show that the plant may belong to the genus *Anadenanthera,* in which case the modern name should be *A. peregrina* (11).

We owe to Spruce the earliest reliable ethnobotanical studies on yopo, although I strongly suspect that some of the present confusion surrounding the use of this snuff may trace back to his writings.

It will be necessary here to diverge for a moment from Spruce's work and consider briefly the state of our knowledge concerning South American narcotic snuffs. Most snuffs used by natives in South America are conveniently identified as being made either from tobacco or from *Piptadenia.* Cooper's distribution map, for example, indicates that *Anadenanthera peregrina* snuff is taken in most of the western Amazon and in many other isolated spots through the Amazon Valley (2). That Cooper himself recognised the unsatisfactory status of our knowledge is evident from his remarks that "some of the attributions may not be correct, since, in some cases, the lack of exact botanical identification makes it doubtful whether we have to do with *Piptadenia* snuff, tobacco snuff or snuff from some other plant . . ." We have now come to suspect (21, 24) that the snuffs used in the Amazon Valley itself are rarely if ever made from this species. In fact, it is now clear that *Anadenanthera peregrina* is a rare plant in the Amazon, where it occurs, for the most part, along the upper Rio


ANADENANTHERA peregrina (L.) Speg.
Fletcher.

Branco or elsewhere rarely. In my long period of botanical exploration in the Amazon, including a number of years in Spruce's territory of the upper Rio Negro basin, I never once met with *Anadenanthera peregrina,* although, as a specialist on native narcotics, I kept a sharp outlook for it. Eight other species referred to *Piptadenia* are known to occur in the Amazon, and I suspect that, in the field, Spruce attributed some of these — not known to have narcotic properties — to his concept of *P. peregrina.* He said ". . . I have traced the tree all the way from the Amazon to the Orinoco, . . . although it bears a different name on the two rivers . . ." The species apparently does not have this distribution now.

Recent ethnobotanical work has uncovered other plants as the sources of psychotomimetic snuffs. One of the most interesting, used in the northwesternmost part of the Amazon, in the upper Rio Negro basin, and adjacent areas of the uppermost Río Orinoco and its tributaries, is prepared from the red resin of the bark of certain species of the myristicaceous genus of *Virola,* especially *V. calophylla* and *V. calophylloidea* (17). I suspect that a species of the acanthaceous genus *Justicia* may be used in the preparation of a snuff of the Waiká Indians of the headwaters of the Orinoco.*** In the central part of the Brazilian Amazon, a psychotomimetic snuff, said to be prepared from the fruits of a jungle tree of the Moraceae, *Olmedioperebea sclerophylla,* has recently been found (20). Other snuffs, as yet unidentified, are known from several localities in South America.

In view of the brevity of Humboldt's report of the preparation of yopo snuff, Spruce's detailed notes acquire much more importance to ethnobotany and phytochemistry. "I did not see the snuff actually prepared from the seeds and

***Very recent investigation has shown that the snuff of the Waiká Indians is prepared basically from *Virola theiodora,* sometimes with the admixture of pulverized leaves of *Justicia pectoralis* var. *sphenophylla* and ashes of the bark of *Elizabetha princeps.* This report was published in Rhodora 70 (1968) 113-160. (R. E. S. July, 1968).

in use until June, 1854, at the cataracts of the Orinoco. A wandering horde of Guahibo Indians, from the river Meta of Colombia, was encamped on the savannahs of Maypures and on a visit to their camp, I saw an old man grinding niopo seeds, and purchased of him his apparatus for making and taking the snuff . . .

"The snuff is kept in a mull made of a bit of the legbone of the jaguar, closed at one end with pitch and at the other end stopped with a cork of marima bark. It hangs around the neck . . .

"The Guahibo had a box of caapi hung from his neck, along with the snuff-box, and as he ground his niopo he every now and then tore off a strip of caapi with his teeth and chewed it with evident satisfaction. 'With a chew of caapi and a pinch of niopo,' said he, in his broken Spanish, 'one feels so good! No hunger — no thirst — no tired!' From the same man, I learnt that caapi and niopo were used by all the nations on the upper tributaries of the Orinoco. . . ."

Much research — ethnobotanical, botanical, phytochemical and pharmacological — has been devoted to yopo snuff. It was probably Spruce's writings more than those of any other investigator, however, that have spurred this research on over the past century.

One of the interesting characteristics about Spruce's writings is that I have never been able completely to understand the paucity of incidental notes on plants with physiological activity. Such long residence amongst the natives of the Amazon might be expected to have enabled Spruce to see so much more that he could report concerning medicinal plants, fish poisons, arrow poisons and other plants of medicinal notice. It may be that Spruce kept such observations in a separate notebook that has been lost, but it is rather more probable that he never dreamed of following up seriously any of these aboriginal uses and, therefore, failed to jot more of them down.

In the two volumes *Notes of a botanist on the Amazon and Andes*, I find no references to any of the arrow or dart

poisons. Nor do I see any mention of plants referred to as fish poison, although this aspect of Indian culture could not have escaped an explorer who lived so long amongst the natives. Furthermore, even though some of the tribes of the upper Rio Negro and Uaupés are known as makers of the most powerful curare preparations or arrow poisons, Spruce is strangely silent on this point. A study of the botanical material amassed on his trips indicates that Spruce did, in fact, collect many of the plants employed in the region as fish poisons or in making curare, but they usually bear no notes regarding these uses. How Spruce, for example, could have failed to discover the use of *Virola* in snuff-making in the uppermost Rio Negro I can never explain, especially when he described as new a number of myristicaceous species.

My own botanical explorations in the northwest Amazon from 1941 through 1953 enabled me to re-trace, in part, Spruce's itinerary. Many are the notes on toxic or medicinal uses that the natives have for plants that Spruce himself collected for the first time and introduced to science with not a note. A few examples will indicate why I am puzzled in this regard.

Spruce collected several species of the genera *Connarus* and *Rourea* in the Rio Negro basin. The roots and stems of these vines are pounded and employed as fish-poisons. Nothing, apparently, is known phytochemically of these uses, nor did Spruce mention them. Spruce collected the type of *Caryocar gracile (Spruce 2550)* of the Caryocaraceae at Ipanoré on the Rio Uaupés. In this region today the leaves of *Caryocar gracile* and other species of the genus are crushed and made into a paste that is administered to dogs for the purpose of killing them when they have once fled with fear in the hunt. Another member of the same family collected by Spruce *(Spruce 2146)* at San Carlos, Venezuela, is *Anthodiscus obovatus*, said to be an ingredient of curare, along with *Strychnos*. Spruce failed to report these relatively important uses of *Caryocar* and *Anthodiscus*. The root of the rubiaceous genus *Duroia* —

especially *D. petiolaris* collected by Spruce — is reputedly toxic. Another genus of this family, *Retiniphyllum*, has the reputation of possessing a toxic resinous exudation from the inflorescence. Spruce collected three species of *Retiniphyllum* in the upper Rio Negro basin — *R. truncatum*, *R. concolor* and *R. speciosum*, all of which are reputedly poisonous, although *R. truncatum* has the reputation of being the strongest. He apparently did not mention the interesting and widespread native belief that the bones of the bird pajuíl *(Nothocrax urumutum)* are toxic to dogs if the bird has eaten the ripened fruit of the apocynaceous tree *Malouetia* (19).

There is, however, so much of value for phytochemistry to be gleaned from Spruce and other contemporary explorers that we should not dwell with too much severity on such minor shortcomings — if, indeed, shortcomings they be. We should here decide to utilise efficiently what they leave us.

We cannot but admire a man like Spruce who, in spite of oppressive sickness, weariness and frustration, was encouraged and spurred on to incredible feats by a dynamic love of knowledge for the sake of knowledge. In a letter to Mr. George Bentham he wrote in part: "I have lately been calculating the number of species that yet remain to be discovered in the great Amazonian forest, from the cataracts of the Orinoco to the mountains of Matto Grosso; taking the fact that by moving away a degree of latitude or longitude I found about half the plants different as a basis, and considering what very narrow strips have, up to this day, been actually explored, and that often very inadequately, by Humboldt, Martius and myself, and others, there should still remain some 50,000 or even 80,000 species undiscovered. To anyone but me and yourself this estimation will appear most extravagant, for even Martius (if I recollect rightly) emits an opinion that the forests of the Amazon contain but few specimens . . .

"At the highest point I reached on the Uaupés, the Jaguaraté Caxoeira, now the boundary line between Brazil and

Colombia, I spent about a fortnight, in the midst of heavy rains, when (according to my constant experience) very few forest trees open their flowers. But when the time came for my return to Panuré . . . . the weather cleared up, and as we shot down among the rocks which there obstruct the course of the river, on a sunny morning, I well recollect how the banks of the river had become clad with flowers, at it were by some sudden magic, and how I said to myself, as I scanned the lofty trees with wistful and disappointed eyes, 'there goes a new *Dipteryx* — there goes a new *Qualea* — there goes a new the Lord knows what! until I could no longer bear the sight and covering up my face with my hands, I resigned myself to the sorrowful reflection that I must leave all these fine things 'to waste their sweetness on the desert air.' From that point upwards, one may safely assume that nearly everything was new, and I have no doubt that the tract of country lying eastward from Pasto to Popayán where are the head-waters of the Japuré, Uaupés, and Guaviare — . . . offer as rich a field for a botanist as any in South America. But I have made enquiries as to the possibility of reaching it, and I find that it will be necessary to cross páramos of the most rugged and inhospitable character, and afterwards risk oneself among wild and fierce Indians, so that I fear its exploration must be left to some one younger and more vigorous than myself."

It is in great part from men like Spruce, that we may continue to expect — even in this commercialised day of high pressure and efficiency — progress in our study of the numberless unknown chemical compounds resident in the vegetation of the world.

BOTANICAL MUSEUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

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THE SPORES OF FOUR SPECIES OF SPINULOSE WOOD FERNS (DRYOPTERIS) IN EASTERN NORTH AMERICA

DONALD M. BRITTON

In a recent paper Nannfeldt (1966) indicated that the diploid *Dryopteris assimilis* S. Walker could be readily distinguished from the tetraploid *Dryopteris dilatata* (Hoffm.) A. Gray by means of spore morphology and the color of the perispore. By using these characters, he was then able to accurately identify these species, and plot their distribution in Sweden. Earlier, Walker and Jermy (1964) emphasized that the spores of *D. assimilis* had a thin pale brown perispore with "widely spaced acute spinnules up to 1μ in length." The spore characters of various species of *Dryopteris* in North America were used by Crane (1963) to construct a key for identification. The data in this paper are presented to compare and contrast the spores of four species of spinulose wood ferns that are found in Eastern North America.

Although there is as yet no unanimity in the names used for these species, or indeed if they should be considered as species, workers are familiar with the names used here. The four taxa considered here as separate species consist of two diploids and two tetraploids. They are the diploid *D. intermedia* (Muhl.) A. Gray, a diploid segregate species allied to *D. dilatata* (Hoffm.) A. Gray which may be conspecific with *D. assimilis* S. Walker, *D. spinulosa* (O. F. Muell.) Watt *(D. carthusiana)*, and *D. campyloptera* Clarkson. *Dryopteris campyloptera* is considered by Wagner (1963) to be an amphidiploid of the first two species, whereas *D. intermedia* is part parental to *D. spinulosa* (Walker 1961). On the basis of cytological and morphological studies, all four species are closely related.

MATERIALS AND METHODS

Sori on mature fronds were gently scraped with a needle dipped in Permount in order to obtain spores. These spores

were then transferred to a drop of Permount on a slide and a cover glass was added. It was usually necessary to put a small weight on the cover glass in order to have a thin enough mount for observation with oil immersion. Measurements of exospore length were made using an ocular micrometer and a 90× apochromatic oil immersion objective. The calibration of the eye-piece was made with the aid of a micrometer slide. The calibration was carefully checked by an independent observer. One ocular division was equivalent to 1.4 microns. It is considered that due to operator error or idiosyncracy that the error in individual measurements is probably ± 1 ocular division or might be considered to be ca. ±1.5 microns.

Whenever possible, cytologically determined material was used for spore measurements. However, this proved impossible for four collections from Mt. Washington, N.H. of *D. campyloptera*, and for five collections of *D. dilatata* from near Lake Superior, Ontario. In these cases, it was necessary to rely on material that was morphologically similar to cytologically determined material from the same limited area, e.g. 12 collections of *D. campyloptera* had been studied cytologically from Mt. Washington (Britton 1962). Voucher Specimens are all at OAC except as indicated for five specimens designated by TRT: (Where no collector is given, the collection is by the author)

D. intermedia *620*, Conc. IV, lot 11, Puslinch Tp., Wellington Co., Ontario, 26 July 1962. *741, 745, 750, 753*, Swan Lake, Algonquin Park, 20 July 1963. *825, 826, 843, 853*, The Beaver Pond, Algonquin Park, Ontario, 15 August 1964. *861*, *H. M. Dale*, 2 mi N of Jefferson Notch near Mt. Washington, N.H. Alt. 2,300 ft., 8 Sept. 1964.

D. dilatata *715, 717*, Garden transplants from N end of Jackfish Lake, Thunder Bay Dist., 25 June 1963. vouchers 23 August 1965. *854, 900, 901*. Garden transplants, *A. Asselin*, Lac Beaudoin, Amos, P.Q. 26 May 1965, vouchers 23 August 1965. (TRT 2, TRT 4), *Taylor, Bannan and Harrison*, Nos. *129, 130*, Port Coldwell, vic. Peninsula, Thunder Bay Dist., 16 August 1939 (TRT). (TRT 6), *Hosie, Losee and Bannan*, No. *89*, Walker Lake, Schreiber, Thun-

der Bay Dist., 11 July 1937 (TRT). (TRT 7), *Taylor et al.*, No. *288*, Mamainse Mt., Algoma Dist., 18 July 1935 (TRT). (TRT 8), *Hosie, Losee and Bannan*, No. *91*, Slate Islands, Thunder Bay Dist., 30 July 1937 (TRT).

D. spinulosa *286*, *290*, Conc. VIII, Lot 20, Puslinch Tp., Wellington Co., Ontario, 22 August 1960. *299*, Conc. III, Lot 15, Puslinch Tp., Wellington Co., 19 August 1960. *305*, Conc. IV, Lot 11, Puslinch Tp., Wellington Co., 19 August 1960. *488*, Conc. IV, Lot 11, Puslinch Tp., Wellington Co., 28 Sept 1961. *504*, Conc. IV, Lot 14, Nelson Tp., Halton Co., 21 Sept 1961. *623*, *624* (see *620*) *716* (see *715* and *717*) *744* (see *741*, *745* etc.)

D. campyloptera *857-860* (see *861*) *971*, Garden Transplant, M. Landon, Yarmouth, N.S. 14 July 1965.

OBSERVATIONS

The average lengths of 20 exospores for each collection of ten plants of each of *D. intermedia, D. dilatata* and *D. spinulosa* and for five plants of *D. campyloptera* are given in Table 1. The extreme measurements for individual spores are shown as well as the overall mean for the species and the range of means of collections.

In Plate 1386, small sections of the perispore are illustrated to show the morphology of some of the spines present.

DISCUSSION

One of the initial decisions, was to decide how many spores of each collection to measure. The measurements of 10, 20, and 30 spores from each of five collections were analyzed by Dr. G. C. Ashton, Dept. of Mathematics. According to the analysis of variance made by him, 20 spores were a suitable number to measure. The 30 spore sample did not yield any further information.

The measurements, together with the morphology show that *D. intermedia* has the most distinctive spores of the four species. The spores of this species are smaller and are covered by long, narrow, sharp spines. The other three species cannot be easily identified by spore characters. These results are not in agreement with those of Wagner

TABLE 1 Lengths of exospores for four species of *Dryopteris*

Species	Collection	Mean length of 20 exospores in microns	Range of lengths in microns
D. intermedia	620	36.3	32-39
	741	34.4	34-39
	745	32.8	31-38
	750	32.2	29-35
	753	35.3	31-39
	825	35.2	28-39
	826	35.9	31-41
	843	36.9	31-42
	853	33.9	31-39
	861	30.9	28-34
	Mean	34.4 (31-37)	28-42
D. dilatata	715	37.4	34-41
	717	36.1	32-41
	854	37.1	34-42
	900	37.4	31-41
	901	36.8	34-41
	TRT2	39.6	35-48
	TRT4	37.8	34-42
	TRT6	37.8	35-39
	TRT7	36.3	34-42
	TRT8	37.1	35-41
	Mean	37.3 (36-40)	31-48
D. spinulosa	286	40.0	35-43
	290	39.8	35-43
	299	35.1	34-38
	305	39.4	36-43
	488	41.0	36-45
	504	36.8	32-42
	623	37.1	34-41
	624	37.0	34-39
	716	37.4	35-42
	744	39.3	36-43
	Mean	38.3 (35-41)	32-45
D. campyloptera	857	41.3	38-43
	858	40.6	36-46
	859	38.6	35-42
	860	39.9	35-45
	971	38.4	35-45
	Mean	39.8 (38-41)	35-46

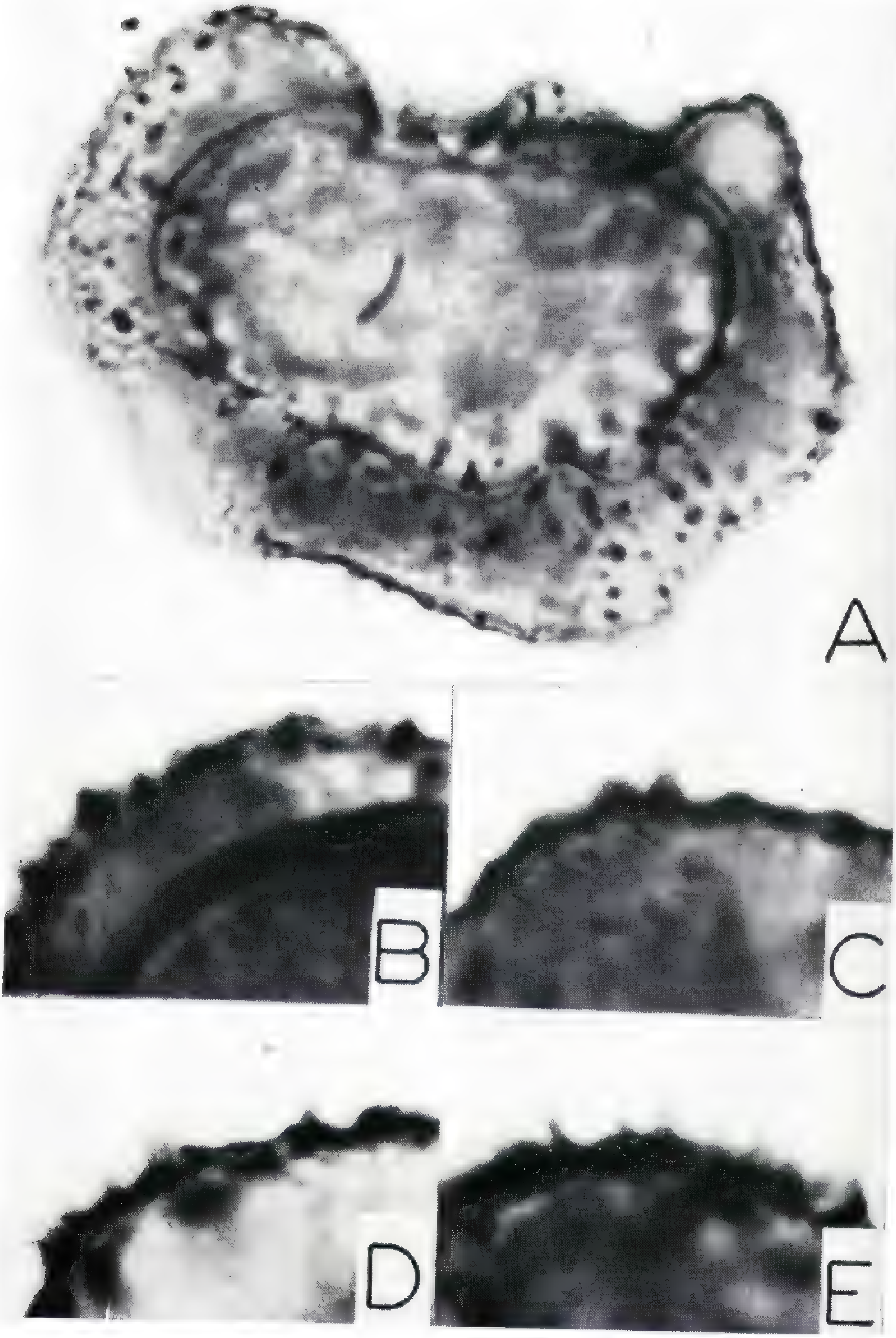

Plate 1386

A, Spore of *Dryopteris intermedia,* × 2000. B-E Portions of perispores to show the morphology of the spines, × 4700: B, *D. dilatata*; C. *D. spinulosa*; D, *D. intermedia*; E, *D. campyloptera.* Note the similarity between B and C and between D and E.

and Hagenah (1962) and Wagner (1963). My results are contrasted with those of these authors in Table 2.

TABLE 2 Mean exospore length and range of means in microns for four species of *Dryopteris*

	D. intermedia	*D. dilatata*	*D. spinulosa*	*D. campyloptera*
Britton	34.4 (31-37)	37.3 (36-40)	38.3 (35-41)	39.8 (38-41)
Wagner	32 (30-32)*	— (33-37)	—	38 (37-40)

*4 collections

As can be seen, Wagner's limited sample of four collections of *D. intermedia* from Virginia had smaller spores. The data are in good agreement for *D. campyloptera*, but differ markedly for *D. dilatata*. It was originally hoped that spore measurements would easily separate the diploid *D. dilatata* from the tetraploid *D. campyloptera*. Such is not the case. Although Wagner and Hagenah (1962) suggest that the averages for individuals of *D. dilatata* will be between 33-37 microns and for *D. campyloptera* from 37-40 microns my data do not support this contention. Eight of the ten collections of *D. dilatata* that were studied had an average exospore length (20 spores) of 37 or greater than 37 microns and none were smaller than 36 microns. Although the average size of all the collections of *D. campyloptera* is greater (39.8) than that of *D. dilatata* (37.3), this does not help in identifying single plants.

Crane (1960) has illustrated the spines of *D. spinulosa* as being blunt. In reality, all are sharp-tipped, but in morphology the sides of the spines are approximately as long as the base is broad, in contrast to the needle-like, narrow-based spines of *D. intermedia*. (Plate 1386)

The spines of *D. dilatata* are widely set and are more similar to those of *D. spinulosa* than to those of *D. intermedia* with its closely set, long, sharp spinnules. The spines of *D. campyloptera* can be visualized as showing the influence of both putative parents, *D. intermedia* and *D. dilatata*. The spines seem slightly longer and more pronounced than those of *D. dilatata* but they are more widely spaced than those of *D. intermedia*. However, the differences are not clear-cut, and it would be difficult to identify one species from another by perispore morphology alone.

Lovis (1964) has discussed the difficulties in obtaining accurate measurements for spore size in *Asplenium*. Calibration of the microscope, mounting medium, operator error and number of spores measured have been mentioned here. Besides these, there is the orientation of the spore on the slide, the possible unconscious selection of the largest spores, spores from sporangia produced late in the season and hence poorly developed, rather than from early sporangia from which the spores were shed. Also, spores from plants growing in very humid conditions versus those growing in drier locations and of course, genetic variability of the individual plants.

However, unlike *Asplenium trichomanes* (Lovis 1964), it would seem that spore size and ploidy are not closely correlated in *Dryopteris*. For example, *D. fragrans* is diploid and has large spores (Crane 1960), and in this paper, the diploid *D. dilatata* has spores which are approximately the size of those of the tetraploids *D. spinulosa* and *D. campyloptera*. Brown (1964) showed in *Woodsia* that the spores of three tetraploid taxa were not larger than those of closely related diploid species. In this respect, *Dryopteris* and *Woodsia* are similar.

CONCLUSIONS

The size of the spores as measured by the length of 20 exospores together with the ornamentation of the perispore allows one to identify diploid *Dryopteris intermedia*. *D. dilatata*, *D. spinulosa* and *D. campyloptera* cannot be easily separated by either spore size or perispore morphology. Accordingly, *D. dilatata* and *D. campyloptera* which have a similar leaf morphology cannot be easily identified. Hence, until further cytological studies are made, identification of *D. dilatata* (2×) and *D. campyloptera* (4×) for the purposes of plotting their distribution is not possible.

The critical cytogenetic evidence is still not available (Britton 1962) to decide the status of the taxon referred to as *D. dilatata*. However, the description of *D. assimilis* given by Walker and Jermy (1964) with particular emphasis on spore characters does not disagree with the spore

characters of the diploid segregate species referred to here as *D. dilatata*. The possibility exists that the diploid segregate species is conspecific with *D. assimilis*.

DEPARTMENT OF BOTANY
UNIVERSITY OF GUELPH
ONTARIO, CANADA

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A MONOGRAPH OF THE GENUS RATIBIDA[1]

EDWARD LEON RICHARDS

The genus *Ratibida*, comprised of six perennial species, one variety, and one color form, is native to southern Canada, the United States, and northern Mexico. The plants inhabit prairies, edge of woodlands, coastal plains, foothills, pine forests and meadows. The meaning of the name *Ratibida*, as far as can be determined, is unknown. *Ratibida columnifera*, *R. pinnata* and *R. tagetes* are sold by nurseries under the name of coneflowers; the other species are of little economical importance. Although Indians of northern Mexico use *R. mexicana* as a wash and potion for bites, rheumatism and other ailments, the plants are of little forage value and are frequently classified as weeds because of their ruderal nature.

This study is the first monographic treatment of *Ratibida* and is based on 3703 specimens from 15 herbaria. Extensive field studies of all taxa from Minnesota to northern Mexico and Colorado to Ohio have afforded the author an opportunity to make population studies and to make more than 300 collections throughout the range of the genus. The completion of this work will add to the knowledge of the genus and provide a basis for future biosystematic study.

Chromosome numbers for the species of *Ratibida* are listed in Table 1. Recorded chromosome counts for the genus are $n = 14$ in *R. columnifera* and *R. peduncularis* var. *picta* (Jackson, 1959), $n = 16$ in *R. tagetes* (Jackson, 1959), $2n = 26, 27$ in *R. columnifera* (Perdue, 1959) and $2n = 28$ in *R. pinnata* (Perdue, 1959). These chromosome numbers were verified during this study from root tip material; counts of other taxa of *Ratibida* not previously recorded are shown in Table 1.

[1]Submitted in partial fulfillment for the degree of Doctor of Philosophy in Botany at the University of Kansas, Lawrence, Kansas.

Table 1. Chromosome Numbers in *Ratibida*

Species	n	Seed Source[1]
R. columnifera *f. columnifera*	14	Ford Co., Kans. *3763*
R. columnifera *f. pulcherrima*	14	Sheridan Co., Kans. *1069*
R. latipalearis	14	Colonia Garcia, Chihuahua, Mex. *D. Spilsbury*
R. mexicana	14	50 km sw. of Guerrero, Chihuahua, Mex. *Hector* and *Raul Sea*
R. peduncularis var. *peduncularis*	14	Willacy Co., Tex. *3743*
R. peduncularis var. *picta*	14	Gonzales Co., Tex. *3728*
R. pinnata	14	Anderson Co., Kans. *3767*
R. tagetes	16	Mora Co., N. Mex. *3773*

[1]Unless otherwise indicated, the numbers quoted are those of the author's collections.

Pollen of all taxa was examined and the only significant difference in stainability was noted in *R. peduncularis* var. *picta* which was 85 percent as compared to 91-97 for the other species. Pollen size for the genus is 17-26 micra as indicated in Table 2. Cotton blue in lactophenol was used and pollen grains taking a full, dark stain were considered viable. Percent of stainability is based on 500 grains for each taxon and measurements of the outside diameter, exclusive of spines, were taken from 50 grains at 430 magnification.

Rafinesque (1817) founded *Ratibida* with a brief description based on *Rudbeckia columnaris* Pursh (1814). In his description, Rafinesque said, "The species with naked seeds such as *Rudbeckia pinnata* Vent. (1800) must form my genus *Obelisteca* and those with a simple perianthe, such

Table 2. Size and Stainability of Pollen in *Ratibida*

Species	Percent Stainable	Size Range in Micra	Average Size in Micra	Sources of Material
R. columnifera f. *columnifera*	97.2	17.1-21.5	19.01	*Richards 3722*
R. columnifera f. *pulcherrima*	94.5	19.8-26.64	24.37	*Richards 3725*
R. latipalearis	93.9	18.2-23.3	20.20	*Richards 3770*
R. mexicana	97.4	18.9-26.64	22.11	*Richards 3768*
R. peduncularis var. *peduncularis*	91.5	19.8-26.9	22.77	*Richards 3739*
R. peduncularis var. *picta*	85.0	18.4-23.1	21.14	*Richards 562*
R. pinnata	95.2	18.9-25.8	22.87	*Richards 3766*
R. tagetes	96.2	18.7-23.3	21.68	*Richards 3764*

as *Rudbeckia columnaris*, must form my genus *Ratibida*." Rafinesque (1819) published a complete description of *Ratibida* and the same year described the genus *Lepachys* based on *Rudbeckia pinnata* Vent. *Lepachys*, a later name than *Ratibida*, is not acceptable under the International Rules of Botanical Nomenclature.

Cassini (1825) described *Obeliscaria* based on *Rudbeckia pinnata* Vent. and deCandolle (1836) treated *Ratibida* and *Lepachys* as synonyms of *Obeliscaria*. *Obeliscaria*, described later than *Ratibida*, is also congeneric with *Ratibida* Raf. Don (1838) recognized *Ratibida* as being the first validly published name for the genus, even though *Lepachys* and *Obeliscaria* were still being used by other authors.

Torrey and Gray (1842) used *Lepachys* for three species and one variety, *L. columnaris*, *L. pinnata*, *L. peduncularis* and *L. columnaris* var. *pulcherrima*. Gray (1852) named *L. peduncularis* var. *picta* and later transferred *Rudbeckia tagetes* James to *Lepachys*. Watson (1888) described *Lepachys mexicana*, and Barnhart (1897) recognized *Ratibida* and rejected *Lepachys* on a priority basis.

The only recent study of the genus was by Sharp (1935) who did a comparative study on all epappose genera of the Heliantheae.

TAXONOMIC CHARACTERS

ROOTS. Fibrous and taproots occur within the genus.

STEMS. The stems are 1.6 to 12.3 dm tall, herbaceous, and branched or unbranched. The leafy branches terminate upward into a naked peduncle. The stems are sulcate with those of *R. mexicana* and *R. latipalearis* averaging 10 ridges, *R. tagetes* 5-6, and all other species 8 ridges.

LEAVES. The leaves of all species are alternate with larger ones at the base and smaller leaves higher up. Petioles on lower leaves are long, becoming short to absent on the uppermost ones. The leaf blades are entire to pinnate, lyrate-pinnate or pinnatifid, linear to lanceolate or obovate.

VESTITURE. The leaves of all species are punctate and hirsute to strigose-hirsute. The trichomes on the lower parts of the stem are up to 1 mm long or longer in *R. mexicana, R. peduncularis, R. pinnata,* and also *R. columnifera* f. *pulcherrima* occurring at high elevations. The remaining taxa possess trichomes of 0.5 mm or shorter. With few exceptions the leaf pubescence is more dense on the lower surface and limited to the veins and margins on the upper surface; stems and peduncles are hirsute to strigose-hirsute on the ridges with unicellular globular glands in the grooves.

PEDUNCLES. Length of the peduncle is important taxonomically as it ranges from 6 cm in *R. tagetes* to 62 cm in *R. mexicana.* The heads are solitary at the ends of naked peduncles.

PHYLLARIES. The herbaceous phyllaries are strigose-hirsute on the outer surface and glabrous to strigose-hirsute only at the tip and along the vein of the inner surface. They are biseriate with the inner 0.1-6.0 mm long, ovate, and the outer series 0.1-14 mm long and linear-lanceolate. Occasionally they appear as a single row or poorly defined double series, e.g. *R. mexicana.*

PALEA. The palea are conduplicate, enclosing the achenes and falling from the receptacle with mature seed in all species except *R. mexicana*. The adaxial edges are hyaline and may be winged or ciliate. The abaxial edges are velutinous-hirsute to about half way down with unicellular glands from the middle to the base in all species except *R. mexicana* which occasionally lacks glands. The tips are recurved and densely velutinous-hirsute, giving the characteristic hoary appearance to the immature heads. A dark resinous linear or oblanceolate gland is along the adaxial edge.

RECEPTACLE. The receptacle is narrow with a tapered apex or oblong with a rounded apex and is usually 2.5 cm or longer in all species other than *R. pinnata* and *R. tagetes*.

RAY COROLLAS. The ray corollas are yellow, yellowish-purple or purple in various species and are all neutral. They are ovate-oblanceolate or lanceolate-oblong with two to three teeth at the apex and reflexed in all species except *R. mexicana* and *R. latipalearis*.

DISC COROLLAS. The disc corollas are fertile, 0.7-2.0 mm long. Each has a light yellowish-green, tubular corolla with purple in the lobes in all species except *R. peduncularis* var. *peduncularis* which has a dark purplish-green apex and *R. latipalearis* with a dark yellow-green apex. They are glabrous except the outer surface of the lobed apex which is velutinous in immature flowers and has globular glands as maturation proceeds. *Ratibida mexicana* has a vertical row of ciliate hairs on the tube opposite the adaxial edge of the palea. Petal segments are distinguishable by a vertical resinous gland from the base of the lobed apex to the base of the tube.

STIGMAS. The stigmas are of taxonomic significance due to variation in the length of the stigmatic surface in various species. At anthesis, the stigmas of *R. mexicana* are greenish-purple, but they are reddish-purple in all other taxa.

PAPPUS. The pappus is a crown or small ring in *R. tagetes*, awn-like or lacking in *R. mexicana* and *R. pinnata*,

and of one to two tooth-like projections in the remaining taxa.

ACHENES. The disc achenes are taxonomically important because of the pubescence on the lateral margins. The adaxial and abaxial margins are glabrous, ciliate or pectinate-fimbriate with the rest of the surfaces glabrous. The base is indented and the shapes vary from linear-oblanceolate to oblong-oblique. Ray achenes are triagonal and strigose-hirsute at the apex.

GENERIC RELATIONSHIPS

Ratibida is a member of the epappose group of the tribe Heliantheae, family Compositae, and is similar to *Echinacea* and *Rudbeckia*. It is closely related to *Rudbeckia* on the basis of columnar receptacles, phyllaries, palea and pappus development. The achenes of *Ratibida* are flattened laterally and are triagonal while in *Echinacea* and *Rudbeckia* they are four-sided. The phyllaries of *Ratibida* are in two series of unequal lengths while *Echinacea* and *Rudbeckia* have two to three series of about equal length. Palea are absent in the columnar receptacle types of *Rudbeckia*, but the phyllaries and palea development of *Ratibida* is similar to *Rudbeckia* (*Dracopsis*) *amplexicaulis*, which some authors consider a distinct genus.

Based on distribution, morphology, method of seed dispersal, and the ruderal nature of the species, Sharp (1935) believed *Rudbeckia* (*Dracopsis*) *amplexicaulis* and *Ratibida* originated from a common ancestor. Anatomically, *Ratibida* and *Rudbeckia* (*Dracopsis*) *amplexicaulis* are similar in stem structure in that the resin canals are opposite the vascular bundles instead of interfascicular as in *Echinacea*. Reported haploid chromosome numbers for *Ratibida* are $n = 16$ and $n = 14$ (Jackson, 1959 and Perdue, 1959); *Rudbeckia* has a reported haploid number of 16, and *Echinacea* has a basic number of $n = 11$ (Darlington and Wylie, 1955).

SYSTEMATIC TREATMENT

RATIBIDA Raf., Flor. Ludovic., p. 73. 1817.

Rudbeckia Linn., Sp. Pl. 906. 1753, in Part.

Obelisteca Raf., Flor. Ludovic., p. 73. 1817.
Lepachys Raf., J. Phys. 89:100. 1819.
Obeliscaria Cass., Dict. Natur. Sci. 35:272. 1825.

Plants perennial with herbaceous stems. Stems simple or branched, mostly erect, strigose-hirsute with vertical light green ridges and dark green grooves containing unicellular-globular glands. Leaves alternate, entire to pinnate, lyrate-pinnate or pinnatifid, linear to lanceolate or obovate, strigose-hirsute with scattered punctate glands interspersed on both surfaces. Heads globular to columnar, solitary on naked peduncles, receptacle linear or oblong; phyllaries reflexed, strigose-hirsute and in two series, a short ovate inner and a longer linear-lanceolate outer series. Ray flowers neutral, yellow, purplish-yellow or purple, reflexed or upright, ovate-oblanceolate to lanceolate-oblong, outer reflexed surface glabrous, inner strigose to hirsute and punctate, apex 2-3-toothed. Disc corollas tubular, greenish-yellow to purplish-green with slight purple at apex, 5-lobed, lobes ovate, reflexed, 0.3-1.0 mm long, 0.3-0.8 mm wide, inner lobe surface velutinous in immature flower but with punctate glands at anthesis; styles short, flat or filiform, style branches short and stigmatic surface a fourth to half the length of the style branches; stamens with sagittate anthers basifixed to short filaments. Palea conduplicate, apex densely velutinous and incurved, adaxial margins hyaline with some ciliation, a small linear to oblanceolate resin gland present on both surfaces near the adaxial edge, abaxial edge velutinous-hirsute to near the middle and glandular to the base, falling at maturity with the achenes except in *R. mexicana*. Achenes glabrous except the edges may be ciliate or pectinate-fimbriate, linear-oblanceolate or oblong-oblique, laterally flattened, with a grooved base. Pappus a crown, or of 1-2 teeth, or lacking.

Native to North America north of the 20th parallel.

Type species. *Ratibida pinnata* (Vent.) Barnhart, Bull. Torr. Bot. Club. 24:410. 1897.

KEY TO THE SPECIES

Plants with fibrous roots, achenes lacking a crown or tooth-like projections.
  Heads columnar; stems unbranched .... 1. *R. mexicana.*
  Heads globular; stems branched .... 2. *R. pinnata.*
Plants with a taproot, achenes with a crown or tooth-like projections.
  Stigmatic surface half the length of the style branch; achenes pectinate-fimbriate on one or two edges.
    Leaves bipinnatifid; achenes pectinate-fimbriate on the edges .... 3a. *R. peduncularis* var. *peduncularis.*
    Leaves lyrate-pinnate; achenes pectinate-fimbriate along only one edge .... 3b. *R. peduncularis* var. *picta.*
  Stigmatic surface one-fourth the length of the style branch; achenes ciliate or glabrous on one edge.
    Heads columnar; pappus of tooth-like projections.
      Rays reflexed; palea longer than broad.
        Rays yellow .... 4a. *R. columnifera* f. *columnifera.*
        Rays purplish-yellow to purple ....4b. *R. columnifera* f. *pulcherrima.*
      Rays upright; palea broader than long .... 5. *R. latipalearis.*
    Heads globular; pappus a crown .... 6. *R. tagetes.*

1. *RATIBIDA MEXICANA* (Wats.) Sharp, Ann. Mo. Bot. Gard. 22:76,77. 1935.

Lepachys mexicana Watson, Proc. Am. Acad. Sci. & Arts 23:277. 1888.

One to several unbranched stems 4.4-9.2 dm tall, pilose-hirsute, spreading above. Leaves ovate-obovate to lanceolate-oblong, basal ones long-petioled, 0.4-2.3 dm long, 1.3-5.6 cm wide, serrate or crenulate, 3-nerved, hirsute below, less so above; upper leaves 2-5 pinnate-parted or cleft, 4.3-16.1 cm long, terminal lobe lanceolate and two-thirds the length of the entire leaf, lateral lobes narrowly oblong or lanceolate, serrate, 0.5-3.3 cm long, 0.1-1.6 cm wide. Peduncles 21.3-61.9 cm long. Heads solitary on naked peduncles, columnar, 1.3-3.2 cm long, 1.0-1.2 cm wide, broader at the base; receptacle linear, tapering at apex. Phyllaries 7-13, 0.4-2.1 cm long, 1.0-2.5 mm wide. Ray flowers 8-15, yellow, oblong or ovate-obovate, 1.5-4.0 cm long, 1.5-11.0 mm wide, outer surface densely hirsute with numerous dark punctate glands, inner surface glabrous, tube 0.8-1.4 mm long, apex 2-3 lobed, 0.1-3.5 mm long, 0.2-2.3 mm wide. Disc corollas 1.8-2.3 mm long, lobes ovate, 0.8-1.0 mm wide, 0.6-1.0 mm long, tube ciliate along one margin; anthers 1.4-2.0 mm long, filaments 0.7-1.0 mm long; styles 1.3-2.0 mm long, the branches 1.0-1.2 mm long, stigmatic surface light yellow, a fourth the length of the style branch. Palea 3.3-5.0 mm long, 1.7-2.1 mm wide, non-deciduous, adaxial edge glabrous or with an occasional unicellular gland, abaxial edge ciliate; resin gland

Plate 1387

Fig. 1. *Ratibida mexicana.* ca. 1/3 actual size. *Richards 3768* (KANU).

linear, 2.2-3.1 mm long. Achenes oblong, 2.6-4.0 mm long, 1.2-3.0 mm wide, glabrous except for occasional ciliate hairs on adaxial edge and apex, pappus lacking. (Figs. 1, 9, 11d, 12d, & 13d).

Flowering time: July-October.

Holotype. Mexico. Chihuahua: cool slopes of the Sierra Madre Occidental, Sept. 19, 1887, *Pringle 1305* GH; Isotype NY!, US!).

Habitat and Distribution. Pine forests and meadows of the Sierra Madre Occidental, Chihuahua, Durango, and Sonora, Mexico.

Ratibida mexicana, occurring at elevations from 6000-9500 feet, is scattered along the Sierra Madre Occidental of northwestern Mexico and has been infrequently collected. Much or this area is accessible only by foot or horse travel and is sparsely populated. The plants are characterized by the upright ligules, unbranched stems, and undivided basal leaves. The Tarahumar Indians refer to the plant as "Howinowa" and crush the roots to use on legs for rheumatism. Other Indian tribes use the roots for a wash and potion and the leaves in a beverage for headaches and colds.

Representative specimens selected from 37 sheets: MEXICO: CHIHUAHUA: *Gentry 2712* (ARIZ, F, GH, MO, UC, US); *Richards 3768* (KANU); *Richards 3769* (KANU); *Townsend & Barber 101* (F, MO, NY, US). DURANGO: *Nelson 4777* (NY, US). SONORA: *Phillips 683* (GH, LL).

2. *RATIBIDA PINNATA* (Vent.) Barnhart, Bull. Torr. Bot. Club. 24:410. 1897.

Rudbeckia pinnata Vent., Desc. Nouv. Pl. Jard. Cels. p. 71. 1800.

Lepachys pinnatifida Raf., J. Phys. 89:100. 1819.

Obeliscaria pinnata (Vent.) Cass., Dict. Sci. Natur. 35:372. 1825.

Lepachys pinnata (Vent.) Torr. & Gray, Fl. N. Am. 2:314. 1842.

Stems one or many, branched, 3.4-12.3 dm tall, hirsute pubescence above. Leaves orbicular-oblong to ovate-oblanceolate or obovate, lower leaves long-petioled, 1.2-3.9 dm long, 1.0-2.5 cm wide, 3-7 pinnate segments, lanceolate-ovate, upper leaves short petiolate or sessile, 0.1-3.1 dm long, segments 3-9, narrowly lanceolate to ovate, 0.1-1.3 dm

Plate 1388

Fig. 2. *Ratibida pinnata.* ca. 1/3 actual size. *Richards 1152* (KANU).

long, 0.2-3.2 cm wide, 3-nerved, serrate or lobed. Peduncles 3.0-26.5 cm long. Heads solitary, globular, 1.1-2.5 cm long, 1.1-1.8 cm wide; receptacle oblong, rounded at apex. Phyllaries 10-14, outer series 0.3-1.1 cm long, 1.0-3.0 mm wide, inner 0.3-0.6 cm long, 1.0-3.0 mm wide. Ray flowers 6-13, yellow, linear to oblong-oblanceolate, 1.6-6.0 cm long, 0.4-1.5 cm wide, outer surface puberulous-hirsute and with punctate glands, inner surface puberulous, apex 2-3 lobed, lobes 0.2-9.0 mm long, 0.2-6.0 mm wide. Disc corollas 1.3-3.0 mm long, lobes 0.6-0.9 mm wide, 0.5-1.0 mm long; anthers 1.7-2.3 mm long, filaments 0.6-1.2 mm long; styles 1.0-2.1 mm long, the branches 1.0-2.0 mm long, stigmatic surface half the length of the style branch. Palea 1.2-5.0 mm long, 1.0-1.8 mm wide, adaxial edge hyaline, entire to ciliate, abaxial edge strigose on upper half and unicellular glands on lower half, resin gland linear, 2.2-3.3 mm long. Achenes linear-oblanceolate, glabrous except for occasional ciliate adaxial edge and apex, 2.4-3.0 mm long, 1.3-2.0 mm wide; pappus lacking. (Figs. 2, 10, 11a, 12a, 13a).

Flowering time: May-October.

Holotype. Illinois: discovered in the country of Illinois by Michaux, grown in Jardin de Cels from seed collected by Michaux (G? Photograph !).

Habitat and Distribution. Edge of woodlands, limestone outcroppings, and prairies. Central and eastern United States and southeastern Canada.

Ratibida pinnata is distributed in Canada and the United States east of the 98th meridian and is less frequent east of the 85th meridian. Colonies can be found along fence rows, edge of woods, banks and ditches. Characteristics of the species are the numerous globular heads, long, yellow ligules, pinnate leaves with coarsely serrate to lobed segments and many branched stems. Because of the similarity in ligules and heads, *R. pinnata* has been confused with *Rudbeckia*.

Representative specimens selected from 789 sheets: UNITED STATES: ALABAMA: Choctaw Co.: *Schuchert*, in 1896 (NY, US). Madison Co.: *Harper 3683* (F, GH, MO, NY, US). Marengo Co.: *McVaugh 8560* (F, GH, TEX). Montgomery Co.: *Howard 12918* (ARIZ, F, GH, KANU, MO, NY, OKL, TEX, UC, US). ARKANSAS: Baxter Co.: *Palmer 6003* (MO, US). Benton Co.: *Richards 1149* (KANU). Carroll Co.: *Richards 1151* (KANU). Clark Co.: *Demaree 17799* (F, MO, OKL). Fulton Co.: *Demaree 26864* (OKL, TEX). Hempstead Co.: *Palmer 8037* (MO). Lawrence Co.: *Demaree 30999* (KANU, OKL). Marion Co.:

Moore 450809 (TEX). Sharp Co.: *Demaree 26894* (KANU, OKL). Washington Co.: *Moore*, in 1927 (TEX). FLORIDA: Jackson Co.: *Wiegand & Manning 3371* (GH). GEORGIA: Bartow Co.: *Duncan 8422* (GH, MO, NY, UC). Catoosa Co.: *Cronquist 5406* (GH, MO, NY, UC, US). Sumter Co.: *Harper 1051* (GH, MO, NY, US). ILLINOIS: Adams Co.: *Evers, Jones & Jones 567* (GH, MO, TEX, UC). Carroll Co.: *Lodewyks 391* (MO). Champaign Co.: *Jones 15307* (MO, TEX, UC). Cook Co.: *Smith 6035* (F, GH, MO, UC). Cumberland Co.: *Richards 1696* (KANU). Du Page Co.: *Umbach 5657* (NY). Fulton Co.: *Chase 10567* (F). Hancock Co.: *Mead*, Augusta (NY). Henderson Co.: *Patterson*, Oquawka (F, MO, NY). Jackson Co.: *Gleason 2802* (GH). Kankakee Co., *De Selm 543* (F). Lake Co.: *Gates 2891* (F). Macon Co.: *Clokey 2406* (F, GH, MO, NY, UC, US). Mason Co.: *Gleason 9222* (NY). McHenry Co.: *Bennett 7971* (F). McLean Co.: *Robinson*, in 1886 (GH). Peoria Co.: *Chase 13497* (F, LL, UC). Pope Co.: *Palmer 17003* (MO). Richland Co.: *Ridgway 742* (GH). St. Clair Co.: *Tesch* (NEB). Sangamon Co.: *Fuller 1367* (F). Stark Co.: *Chase 709* (F, MO). Whiteside Co.: *Reecher 219* (F). Will Co.: *Swink 2453* (F). Winnebago Co.: *Bebb 3508* (MO). INDIANA: DeKalb Co.: *Shoop*, in 1933 (F). Delaware Co.: *Brady*, in 1888 (UC). Elkhart Co.: *Ek*, in 1942 (F, MO). Greene Co.: *Springer 825* (KANU, NEB, TEX). Jasper Co.: *Welch 1821* (GH, MO). Lagrange Co.: *Perdue 2062* (LL). La Porte Co.: *Coulter*, in 1878 (F, GH). Lawrence Co.: *Kriebel 2314* (GH). Marion Co.: *Floyd*, in 1887 (F). Marshall Co.: *Stovell & Walton 823* (US). Newton Co.: *Friesner 14707* (NY, UC). Noble Co.: *Brooks 2595* (KANU). Porter Co.: *Swink 1772* (F). St. Joseph Co.: Coll. unknown (*E.B.U.*), in 1891 (F). Union Co.: *Rose*, in 1886 (F). Wabash Co.: *Friesner 9006* (F, TEX). Wells Co.: *Deam 1370* (MO, NY, US). IOWA: Adams Co.: *Richards 1264* (KANU). Audubon Co.: *Richards 1296* (KANU). Black Hawk Co.: *Burk 556* (MO). Buena Vista Co.: *Richards 1276* (KANU). Carroll Co.: *Richards 1272* (KANU). Cass Co.: *Richards 1267* (KANU). Cedar Co.: *Pammel 712* (GH). Clay Co.: *Richards 1277* (KANU). Clayton Co.: *Shimek*, in 1923 (NY). Dallas Co.: *Allen*, in 1867 (GH, MO). Decatur Co.: *Anderson*, in 1904 (MO). Dickinson Co.: *Richards 1281* (KANU). Emmet Co.: *Cratty*, in 1897 (MO, US). Fayette Co.: *Fink 545* (US). Harrison Co.: *Fay 3678* (KANU). Iowa Co.: *Easterly 757* (ARIZ). Johnson Co.: *Loufek*, in 1938 (NY). Madison Co.: *Shimek*, in 1917 (MO). Mahaska Co.: *Augustine 377* (OKL). Monona Co.: *Gleason 9324* (NY). Montgomery Co.: *Richards 1265* (KANU). Muscatine Co.: *Shimek*, in 1910 (F, MO). O'Brien Co.: *Shimek*, in 1929 (NY). Osceola Co.: *Richards 1282* (KANU). Pottawattamie Co.: *Bates 437* (NEB). Poweshiek Co.: *Rohrbaugh 100* (OKL, TEX). Ringgold Co.: *Richards 1261* (KANU). Sac Co.: *Richards 1274* (KANU). Story Co.: *Pammel & Ball 56* (CS, F, GH, MO, NY, US). Taylor Co.: *Richards 1263* (KANU). Union Co.: *Richards 1262* (KANU). Washington Co.: *Wagenknecht 568* (F).

Webster Co.: *Somis 3892* (NEB). Winneshick Co.: *Tolstead,* in 1933 (MO). Woodbury Co.: *Hayden 10783* (UC). KANSAS: Allen Co.: *Richards 1137* (KANU). Anderson Co.: *Richards 1134* (KANU). Atchison Co.: *Horr 4468* (GH, KANU). Bourbon Co.: *Thompson,* Hammond (KANU). Brown Co.: *Horr 4486* (GH). Cherokee Co.: *McGregor 15802* (KANU). Coffey Co.: *Richards 1080* (KANU). Doniphan Co.: *Horr 4261* (KANU). Douglas Co.: *Richards 3766* (KANU). Franklin Co.: *Richards 3752* (KANU). Greenwood Co.: *Englemann 1033* (OKL). Jefferson Co.: *Richards 1255* (KANU). Johnson Co.: *McGregor 4381* (GH, KANU). Labette Co.: *Rydberg & Imler 310* (KANU, NY). Leavenworth Co.: *Richards 1256* (KANU). Linn Co.: *Richards 3754* (KANU). Lyon Co.: *McGregor 14071* (KANU). Montgomery Co.: *Richards 1139* (KANU). Neosho Co.: *Richards 3166* (KANU). Shawnee Co.: *Norton & Clothier 266* (GH, MO, NY, US). Wabaunsee Co.: *McGregor 14073* (KANU). Wilson Co.: *Horr,* in 1930 (KANU). Woodson Co.: *Horr & McGregor,* in 1947 (KANU). Wyandotte Co.: *Richards 3256* (KANU). KENTUCKY: Bullitt Co.: *Bishop 386* (GH). Edmondson Co.: *Lix,* in 1947 (US). Jefferson Co.: *Gunn J-165, 1655* (MO, NY). Logan Co.: *Gleason 8929* (NY). Mercer Co.: *King 125* (F). Scott Co.: *Singer 364* (US). Warren Co.: *Price,* in 1900 (MO). LOUISIANA: La Salle Parish: *Shinners 23990* (GH, TEX). MASSACHUSETTS: Berkshire Co.: *Britton,* in 1909 (NY). MICHIGAN: Calhoun Co.: *Parmelee 2901* (TEX). Ingham Co.: *Parmelee 700* (TEX). Jackson Co.: *Camp & Camp,* in 1897 (F, US). Kalamazoo Co.: *Burgess 378* (F). Kent Co.: *Crozien,* in 1886 (NY). Mackinac Co.: *Ehlers 281* (GH). Washtenaw Co.: *Hermann 9067* (NY). Wayne Co.: *Chandler,* in 1917 (US). MINNESOTA: Cass Co.: *Richards 1406* (F). Cottonwood Co.: *Richards 1285* (KANU). Dodge Co.: *Jeffs,* in 1908 (OKL). Hennepin Co.: *Sandberg,* in 1889 (F, NY, UC). Mower Co.: *Brenckle 47-537* (NY). Murray Co.: *Richards 1288* (KANU). Nicollet Co.: *Ballard,* in 1892 (NY, UC, US). Nobles Co.: *Richards 1284* (KANU). Pipestone Co.: *Richards 1290* (KANU). Ramsey Co.: *Churchill,* in 1912 (MO). Rice Co.: *Hutchinson 47* (NEB). Rock Co.: *Richards 1295* (KANU). Winona Co.: *Holzinger,* in 1905 (NY). MISSISSIPPI: Lowndes Co.: *Diener 934* (NY). Oktibbeha Co.: *Tracy,* in 1892 (US). MISSOURI: Barry Co.: *Richards 1148* (KANU). Benton Co.: *Richards 3340* (KANU). Butler Co.: *Eby,* in 1893 (MO). Camden Co.: *Chandler 4731* (MO). Carter Co.: *Palmer 6204* (MO, US). Cass Co.: *Richards 3312* (KANU). Clay Co.: *Mackenzie 262* (MO, NY). Dallas Co.: *Richards 1162* (KANU). Douglas Co.: *Richards 3401* (KANU). Franklin Co.: *Kellogg 1283* (MO). Greene Co.: *Standley 9622* (US). Henry Co.: *Hitchcock,* Windsor Springs (MO). Hickory Co.: *Richards 1163* (KANU). Jackson Co.: *Bush 164* (MO, NY, OKL, US). Jasper Co.: *Richards 3437* (KANU). Jefferson Co.: *Steyermark 1036* (MO). Johnson Co.: *Richards 1167* (KANU). Laclede Co.: *Richards 1160*

(KANU). Lincoln Co.: *Davis 2732* (MO). Livingston Co.: *Sparling 111* (F). Marion Co.: *Davis 7260* (MO). Mercer Co.: *Palmer & Steyermark 41291* (GH, MO). Nodaway Co.: *Richards 1258* (KANU). Ozark Co.: *Richards 1156* (KANU). Pettis Co.: *Richards 1166* (KANU). Phelps Co.: *Steyermark 72173* (F). Pulaski Co.: *Dixon*, in 1928 (MO). Ralls Co.: *Davis 4645* (MO, TEX). St. Clair Co.: *Bush 12797* (MO). St. Francois Co.: *Bower 17* (F). St. Louis Co.: *Sherff 68* (GH). Saline Co.: *Marsh 1629* (NY). Shannon Co.: *Bush 6147* (MO). Stone Co.: *Richards 3415* (KANU). Taney Co.: *Richards 3387* (KANU). Wright Co.: *Richards 3347* (KANU). NEBRASKA: Cass Co.: *Richards 1308* (KANU). Dakota Co.: *Richards 1306* (KANU). Dodge Co.: *Richards 1307* (KANU). Douglas Co.: *Cleburne*, Omaha (NEB). Nemaha Co.: *Webber 6086* (NEB). Otoe Co.: *Richards 1309* (KANU). Sarpy Co.: *Prind & Saunders 3126* (NEB). Saunders Co.: *Williams*, Ashland (US). NEW YORK: Chautaqua Co.: *Sartwell* (GH). Yates Co.: *Sartwell* (F). OHIO: Adams Co.: *Stephenson*, in 1930 (MO). Delaware Co.: *Crane 2447* (NY). Erie Co.: *Moseley*, in 1895 (GH, US). Franklin Co.: *Condit*, in 1909 (UC). Greene Co.: *Demaree 11477* (MO, US). Ross Co.: *Bartley & Pontius 49* (NY). OKLAHOMA: Adair Co.: *Waterfall 9676* (KANU). Cherokee Co.: *Teachers College*, in 1924 (OKL). Craig Co.: *Stevens 2207* (GH). McCurtain Co.: *Clark 2946* (OKL). Muskogee Co.: *Waterfall 9514* (KANU). Nowata Co.: *Richards 1144* (KANU). Ottawa Co.: *Stevens 2283* (GH, MO, NY, OKLA, US). SOUTH DAKOTA: Clay Co.: *Richards 1305* (KANU). Codington Co.: *Johnson 78* (GH, TEX). Minnehaha Co.: *Richards 1299* (KANU). Roberts Co.: *Johnson* (MO, NY). TENNESSEE: Davidson Co.: *Ward*, in 1877 (US). Franklin Co.: *Eggert*, in 1898 (MO, NY). Lewis Co.: *McDougall 1411* (US). Marshall Co.: *Bain*, in 1892 (US). Maury Co.: *Shimek*, in 1891 (F, MO). Meigs Co.: *Sharp & Underwood 2331* (MO, UC). Rutherford Co.: *Demaree 45751* (KANU). Warren Co.: Coll. unknown *2639* (US). Wilson Co.: *Svenson 9588* (GH, UC). VERMONT: Chittenden Co.: *Wright 2040* (MO). WISCONSIN: Brown Co.: *Schuette*, in 1884 (F, GH, NY, US). Buffalo Co.: *Fassett & Wilson 4467* (GH). Dane Co.: *Seymour 1084* (KANU). Door Co.: *Millspauth 3691* (F). La Crosse Co.: *Hartley 997* (US). Milwaukee Co.: *Hasse* (UC). Outagamie Co.: *Melchert*, in 1960 (TEX). Sauk Co.: *Eggert*, in 1903 (MO). Walworth Co.: *Shannon 133a* (MO). Winnebago Co.: *Kellerman* (US). CANADA: ONTARIO: *Macoun 34829* (GH, MO, NY, US).

3. *RATIBIDA PEDUNCULARIS* (Torr. & Gray) Barnhart, Bull. Torr. Bot. Club. 24:411. 1897.

Stems one or many, branched, 2.8-11.2 dm tall, thickly hirsute near the base. Leaves oblong-obovate, bipinnatifid to lyrate-pinnate, 1.6-13.7 cm long, 1.0-6.4 cm wide, leaf divisions 3-10, 0.3-6.0 cm long, lobes 0.8-4.3 mm wide. Peduncles 14.8-45.5 cm long. Heads solitary,

Plate 1389

Fig. 3. *Ratibida peduncularis* var. *peduncularis*. ca. 1/3 actual size. *Richards 3742* (KANU).

columnar, 1.7-6.9 cm long, 0.8-1.3 cm wide; receptacle linear, tapering at the apex. Phyllaries 7-14, outer series 0.6-1.2 cm long, 0.8-1.3 mm wide, inner 0.1-0.5 cm long, 0.9-1.2 mm wide. Ray flowers 6-13, linear-oblong to oval-orbicular, yellow, purplish-yellow and purple, 4.0-13.5 mm long, 3.0-10.0 mm wide, outer surface hirsute and with unicellular-globular glands, inner glabrous, tube 1.0 mm long, apex 2-3 lobed, lobes 0.2-6.0 mm long, 0.2-3.0 mm wide. Disc corollas 1.5-2.5 mm long, the lobes 0.6-0.8 mm wide, 0.5-0.8 mm long; anthers 1.3-2.0 mm long, filaments 0.5-1.0 mm long; styles 1.0-2.0 mm long, the branches 0.5-2.0 mm long, stigmatic surface half the length of the style branches. Palea 3.0-4.3 mm long, 1.5-3.0 mm wide, adaxial side ciliate, abaxial edge ciliate half way down and with unicellular glands to base, resin gland oval, 1.0-1.8 mm long. Achenes oblique-oblong, 2.3-5.0 mm long, 1.2-3.0 mm wide, margin pectinate-fimbriate, edges winged; pappus of one to two teeth.

3a. *R. PEDUNCULARIS* (Torr. & Gray) Barnh. var. *PEDUNCULARIS*.

Lepachys peduncularis Torr. & Gray, Flora N. Am. 2:315. 1842.

Obeliscaria peduncularis (Torr. & Gray) Walp., Repert. 2:979. 1843.

Leaves bipinnatifid, ovate-oblong, 2.1-11.2 cm long, 1.1-4.0 cm wide, segments 4-10, linear-lanceolate to ovate-obovate, 0.1-3.2 cm long, 0.1-1.1 cm wide; hairs on upper part of stem with raised base. Achenes pectinate-fimbriate on both edges. Ray flowers yellow to purplish-yellow. (Figs. 3, 10, 11g, 12g, 13g).

Flowering time. March-November.

Lectotype. Texas: S. Felipe de Austin, in 1835, *Drummond 108* (GH!). Since Torrey and Gray did not select a type from the original material, the above lectotype was selected by the author.

Habitat and Distribution. Sandy coastal plains of southeastern Louisiana, Texas, and northeastern Tamaulipas, Mexico.

Ratibida peduncularis var. *peduncularis* occurs mainly on the coastal plains of Louisiana, Texas and Mexico. The coastal forms are usually characterized by yellow or purplish-yellow ligules while those more inland have purplish-yellow ligules. Typically the plants have dissected leaves, long peduncles, and achenes with pectinate-fimbriate margins.

Plate 1390

Fig. 4. *Ratibida peduncularis* var. *picta*. ca. 1/3 actual size. *Richards 3732* (KANU).

Representative specimens selected from 69 sheets: UNITED STATES: LOUISIANA: Cameron Parish: *Tracy 8548* (F, MO, NEB, NY, TAES). TEXAS: Aransas Co.: *Richards 3739* (KANU). Bexar Co.: *Schulz 422* (TEX, US). Brooks Co.: *Richards 3744* (KANU). Calhoun Co.: *Parks & Cory 11644* (TAES). Cameron Co.: *Runyon 441* (US). Dimmit Co.: *Hamby 950* (LL). Galveston Co.: *Wright* (US). Goliad Co.: *Beamer,* in 1953 (KANU). Hidalgo Co.: *McKelvey 1751* (GH). Jim Hogg Co.: *Lehmann & Davis 38* (F). Kenedy Co.: *Richards 3741* (KANU). Kleberg Co.: *Johnston 54422* (TAES, TEX). Nueces Co.: *Heller 1789* (GH, MO, NY, UC, US). Orange Co.: *Small & Wherry 11802* (NY, US). San Patricio Co.: *Cory 49140* (GH). Willacy Co.: *Richards 3743* (KANU). MEXICO: TAMAULIPAS: *LeSueur 509* (F, TEX).

3b. *R. PEDUNCULARIS* (Torr. & Gray) Barnh. var. *PICTA* (Gray) Sharp, Ann. Mo. Bot. Gard. 22:74. 1935.

Lepachys peduncularis Torr. & Gray var. *picta* Gray, Smiths. Contr. Knowl. (Pl. Wright.) 3:107. 1852.

Lepachys serratus Buckl., Acad. Natur. Sci. Phila. 13:457. 1861.

Ratibida picta (Gray) Small, Flora S. E. United States, ed. 1, 1260 p. 1903.

Leaves lyrate-pinnate, ovate-obovate or oblong, 1.6-13.7 cm long, 1.0-6.4 cm wide, segments 3-7, terminal lanceolate-ovate, toothed to parted, 0.6-7.2 cm long, 0.3-5.0 cm wide, lateral segments linear-oblong to obovate, 0.1-4.5 cm long, 0.1-1.4 cm wide; long pilose and hirsute hairs on lower stem becoming shorter and more numerous on upper stem with the longer hairs strigose, punctate glands mostly few or absent. Achenes pectinate-fimbriate on adaxial edges. Ray flowers purplish-yellow to purple. (Figs. 4, 10, 11e, 12e, 13e).

Flowering time: April-October.

Lectotype. Texas: Gulf Coast near Galveston, in 1849, *Wright* (GH!). Since Gray did not select a type from the original material, the above lectotype was selected by the author.

Habitat and Distribution. Sandy seacoast and wooded areas of the Texas coastal region.

Ratibida peduncularis var. *picta* is limited in distribution to the seacoast and inland coastal woods of Texas. This variety is recognized because of the lyrate-pinnate leaves and the pectinate-fimbriate adaxial margin of the achenes.

The achenes are usually more narrow and the unicellular globular glands on the stems and peduncles are less frequent than in *R. peduncularis* var. *peduncularis*. The range overlaps with that of *R. columnifera* and the two species readily hybridize (Jackson, 1963).

Ratibida peduncularis var. *picta* probably hybridizes with *R. peduncularis* var. *peduncularis* where their ranges overlap. Collections seem to indicate this as plants intermediate in leaf and achene characteristics and usually more robust than either of the above have been found (*Richards 3745*, KANU).

Representative specimens selected from 52 sheets: UNITED STATES: TEXAS: Aransas Co.: *Richards 3737* (KANU). Bexar Co.: *Richards 3735* (KANU). Calhoun Co.: *Tharp 5639* (TEX, US). Frio Co.: *Higdon* s.n. (TEX). Gonzales Co.: *Richards 3730* (KANU). Guadalupe Co.: *Richards 3731* (KANU). Harris Co.: *Thurrow,* in 1890 (F). Medina Co.: *Richards 3745* (KANU). Victoria Co.: *Tracy 8941* (F, GH, MO, NEB, NY, TAES, TEX). Waller Co.: *Hall 336* (F, MO, NY, US). Wilson Co.: *Richards 3734* (KANU).

4. *RATIBIDA COLUMNIFERA* (Nutt.) Woot. & Standl. Contrib. U. S. Nat. Herb. 19:706. 1915.

Stems one or many, branched, 2.2-10.4 dm high. Leaves ovate-obovate to orbicular-oblanceolate, 1.8-15.1 cm long, 0.8-6.0 cm wide, bipinnatifid, segments 3-14, narrowly linear-lanceolate to ovate-oblong, 0.1-6.0 cm long, 0.1-1.6 cm wide. Peduncles 1.4-47.3 cm long. Heads solitary, columnar, 1.0-4.7 cm long, 0.7-1.2 cm wide. Phyllaries 5-14, the inner row lanceolate-ovate, 0.8-2.0 mm long, 0.8-1.8 mm wide, outer linear, 0.4-1.4 cm long, 0.5-2.0 mm wide. Ray flowers 4-11, yellow, purplish-yellow to purple, ovate-oblanceolate to oblong-elliptical, 0.7-3.5 cm long, 0.4-1.7 cm wide, inner surface glabrous to puberulent, outer surfaces hirsute, punctate, apex 2-3 lobed, lobes 0.1-5.3 mm long, 0.2-7.1 mm wide. Disc corollas 1.6-2.8 mm long, lobes 0.5-1.0 mm wide, 0.3-0.8 mm long; anthers 1.2-1.9 mm long, filaments 0.4-1.0 mm long; styles 0.8-1.5 mm long, the branches 0.5-1.4 mm long, stigmatic surface a fourth the length of the branch. Palea 2.3-3.5 mm long, 0.5-3.0 mm wide, adaxial edge hyaline, ciliate, abaxial edge strigose from apex to middle, unicellular glands from middle to base; resin gland oval-oblanceolate, 0.6-1.5 mm long. Achenes oblong, 1.2-3.0 mm long, 1.2-2.0 mm wide, glabrous except for the ciliate adaxial edge and ciliate or squamellous apex; pappus of 1-2 teeth or absent.

Plate 1391

Fig. 5. *Ratibida columnifera* f. *columnifera*. ca. 1/3 actual size. *Richards 1019* (KANU).

4a. *RATIBIDA COLUMNIFERA* (Nutt.) Woot. & Standl. forma *COLUMNIFERA*.

Rudbeckia columnifera Nutt., Fraser's Catal. 1813.

Rudbeckia columnaris Pursh, Flora Am. Sept. 2:575. 1814.

Ratibida sulcata Raf. J. Phys. 89:100. 1819.

Obeliscaria columnaris DeCandolle Prodr. 5:559. 1836.

Ratibidia columnaris (Sims) D. Don, Sweet's Brit. Fl. Gard. 4:361. 1838.

Lepachys columnaris Torr. & Gray, Flora N. Am. 2:315. 1842.

Lepachys columnifera (Nutt.) MacBride, Contrib. Gray Herb. New Ser. 3(65):45. 1922.

Ratibida columnifera (Nutt.) Woot. & Standl. var. *breviradiata* Cockerell, Am. Natur. 49(586):620. 1915.

Ratibida columnifera (Nutt.) Woot. & Standl. var. *incisa* Cockerell, Am. Natur. 49(586):620. 1915.

Ratibida columnifera (Nutt.) Woot. & Standl. var. *tubularis* Cockerell, Am. Natur. 49(586):620. 1915.

Ratibida columnifera (Nutt.) Woot. & Standl. var. *appendiculata* Cockerell, J. Hered. 7:428. 1916.

Ratibida columnaris (Pursh) Raf. forma *denudata* Boivin, Natur. Can. 87:49. 1960.

Flowering time. March-November.

Holotype. As far as can be ascertained, there are no known types. Evidence indicates that the plants were first collected from the "country of the Missourie", 1813. *Nuttall.*

Habitat and Distribution. Prairies and foothills. Southern Canada, United States, and northern Mexico.

Rudbeckia columnifera Nutt. was first published in Fraser's Catalogue in 1813. While there is some dispute as to the authorship and legality of the Catalogue, I am accepting Nuttall as the author, at least of the plants accompanied with descriptions. This opinion is based on my studies of several of Nuttall's works plus additional papers favoring him as the author. These are as follows: Dress (1961), Cronquist *et al* (1956), Fernald (1938), Britten

(1899) and Greene (1890). Britten (1899) states that the list of names in the Catalogue was written by Nuttall who added his name in ink to the copy from which Professor Greene's reprint was made. Greene (1890) says: "Nuttall wrote his name in ink as the author and even made a few corrections on the copy of the catalogue which was used for the reprint in Pittonia." Nuttall (1818) refers 22 times to his names in "Fraser's Catalogue". Nuttall (1841), writing on *Aplopappus spinulosus*, states: "to which I applied the name of *Sideranthus* in "Fraser's Catalogue." Sims (1814) used plants grown at Fraser's nursery and credits Nuttall as introducing them from the "country of the Missourie". Pursh (1814) cites *Rudbeckia columnifera* Nutt. as a synonym for *Rudbeckia columnaris*. While the description of *Rudbeckia columnifera* in the catalogue is meager, Fernald (1938) sums it up by saying: "certainly this is a far more intelligible diagnosis of a species than was the original characterization of *Ratibida* for a genus." Cronquist *et al* (1956) recognized the names with descriptions in "Fraser's Catalogue" as being validly published. The author accepts *Ratibida columnifera* (Nutt.) Woot. and Standl. as the legitimate name.

Cockerell (1915) described three varieties of *Ratibida columnifera* from Boulder, Colorado, as follows: var. *breviradiata* (US) with short rays, 10 mm long; var. *incisa* (US) with emarginate and cleft rays; var. *tubularis* with rays 25 mm long and 3.5 mm wide, completely quilled, being hollow cylinders. The three varieties named by Cockerell have all been observed over the range of the species by me and are not recognized as varieties, although their occurrence may be uncommon. Aberrant and teratological forms of many kinds have been observed and it is my opinion that they should not be afforded taxonomic rank.

Cockerell (1916) described *Ratibida columnifera* (Nutt.) Woot. & Standl. var. *appendiculata* (GH) with the rays possessing long appendages (usually paired) arising from the throat. Similar aberrant forms have been observed by the author and this variety is not recognized in this study.

Boivin (1960) described *Ratibida columnaris* (Pursh) Raf. forma *denudata* (*Boivin* & *Alex 9886* DAO) where the head was devoid of ray flowers. Even though this condition apparently is not a common occurrence in the above species, it is not recognized in this study.

Ratibida columnifera is the most widespread species of the genus and exhibits many morphological forms over its range. Plants of the prairies are characterized by being tall and robust with long, columnar heads while those of drier areas as well as those growing later in the season tend to be shorter and have shorter heads. In sandy areas the plants are more annual, shorter, and less branched. In the southern part of the range, the ligules tend to be somewhat shorter as are those growing later in the season and in dry areas. In ruderal areas, the plants may assume a "bushy" appearance with much branching and short heads. Typically, the species is characterized by the columnar head, yellow ligules, and bipinnatifid leaves.

Representative specimens selected from 1,489 sheets: UNITED STATES: ARIZONA: Apache Co.: *Palmer 601* (GH, NY, US). Coconino Co.: *MacDougal 416* (GH, KANU, NY, US). Navajo Co.: *Mayerhoff 59* (F). ARKANSAS: Crittenden Co.: *Demaree 11380* (MO). Washington Co.: *Palmer 8216* (MO, NY). COLORADO: Adams Co.: *Johnston 217A* (MO). Arapahoe Co.: *Clokey 2819* (MO). Baca Co.: *Harrington 3311* (CS). Boulder Co.: *Hanson C139* (ARIZ, MO). Chaffee Co.: *Sheldon 472* (US). Cheyenne Co.: *Christ 983* (CS). Denver Co.: *Clokey 2819* (ARIZ, F, GH, UC). Douglas Co.: *Christ 1145* (CS). Elbert Co.: *Woodward*, in 1882 (GH). El Paso Co.: *Ehlers 7717* (ARIZ, GH). Fremont Co.: *Brandegee 757* (NY). Jefferson Co.: *Cleburne*, in 1914 (NEB). Kiowa Co.: *Harrington 4263* (CS). Kit Carson Co.: *Preston*, Vona (CS). Larimer Co.: *Marshall 2985* (CS, NEB, US). Las Animas Co.: *Rogers 4428* (US). Lincoln Co.: *Harrington 792* (CS). Phillips Co.: *Harrington 2255* (CS). Prowers Co.: *Harrington 3480* (CS). Pueblo Co.: *Mathias 526* (MO). Washington Co.: *Shantz 1133* (US). Weld Co.: *Johnston 217* (MO). Yuma Co.: *Harrington 4242* (CS). IDAHO: Bannock Co.: *Sharpe 17204* (NY). Power Co.: *Christ & Ward 15030* (NY). ILLINOIS: Cook Co.: *Gates 1221a* (F). Du Page Co.: *Umbach* (F, US). Madison Co.: *Eggert*, in 1891 (MO). Menard Co.: *Hall*, in 1861 (F). Peoria Co.: *Chase 8923* (KANU, OKL). INDIANA: Clark Co.: *Lansing 981* (F). IOWA: Clay Co.: *Hayden 10784* (NY). Dickinson Co.: *Shimek*, Milford (NEB). Fremont Co.: *Harms 616* (KANU). Linn Co.: *Smith*, in 1871

(NY). Lyon Co.: *Gleason 9370* (NY). Muscatine Co.: *Shimek,* in 1915 (MO). Polk Co.: *Hayden 10546* (MO, NEB, NY, TEX). Pottawatomie Co.: *Shimek,* in 1909 (F, NY). Sioux Co.: *Hayden 10547* (GH, MO, NY, UC). Webster Co.: *Somis 3893* (NEB). Woodbury Co.: *Thorne 13366* (US). KANSAS: Anderson Co.: *Richards 1133* (KANU). Barber Co.: *Richards 792* (KANU). Barton Co.: *Richards 876* (KANU). Bourbon Co.: *Thompson* (KANU). Butler Co.: *Richards 1086* (KANU). Chase Co.: *Richards 1082* (KANU). Chautauqua Co.: *Hulbert 3162* (KANU). Cheyenne Co.: *Horr 4692* (GH, KANU). Clark Co.: *Richards 835* (KANU). Clay Co.: *McGregor 5015* (KANU). Cloud Co.: *Kellerman,* in 1888 (MO). Coffey Co.: *Richards 1081* (KANU). Comanche Co.: *Richards 822* (KANU). Cowley Co.: *Richards 1087* (KANU). Decatur Co.: *Richards 2835A* (KANU). Dickinson Co.: *Hulbert 3164* (KANU). Douglas Co.: *Richards 3765* (KANU). Edwards Co.: *McGregor 10556* (KANU). Elk Co.: *Richards 687* (KANU). Ellis Co.: *Richards 1074* (KANU). Ellsworth Co.: *Richards 1076* (KANU). Finney Co.: *Coville 25* (US). Ford Co.: *Richards 3763* (KANU). Franklin Co.: *Richards 3753* (KANU). Geary Co.: *Richards 1077* (KANU). Gove Co.: *Horr & McGregor 3262* (GH, KANU). Graham Co.: *Richards 1071* (KANU). Grant Co.: *Thompson 15* (F, GH, MO, NY, UC, US). Greeley Co.: *Rose & Fitch 17076* (NY, US). Greenwood Co.: *Richards 654* (KANU). Hamilton Co.: *Richards 865* (KANU). Harper Co.: *Richards 772* (KANU). Harvey Co.: *McGregor 12515* (KANU). Hodgeman Co.: *McGregor 10597* (KANU). Jefferson Co.: *Marsh 1615* (KANU, US). Jewell Co.: *Horr 4363* (KANU). Kearney Co.: *Richards 871* (KANU). Kingman Co.: *McGregor 10708* (KANU). Kiowa Co.: *Horr 3989* (KANU). Labette Co.: *Richards 1140* (KANU). Lincoln Co.: *McGregor 7444* (KANU). Linn Co.: *Richards 3755* (KANU). Logan Co.: *McGregor 9405* (KANU). Lyon Co.: *McGregor 1868* (KANU). Marion Co.: *Richards 1084* (KANU). Marshall Co.: *Heller 13975* (MO). McPherson Co.: *Richards 879* (KANU). Meade Co.: *Richards 844* (KANU). Miami Co.: *Oyster 4149* (F, MO, NY). Montgomery Co.: *Rydberg & Imler 366* (KANU, MO). Morris Co.: Horr, in 1930 (KANU). Morton Co.: *Richards 2966* (KANU). Neosho Co.: *Richards 3182* (KANU). Norton Co.: *Richards 2793* (KANU). Osborne Co.: *Shear 121* (GH, NEB, US). Pawnee Co.: *Richards 874* (KANU). Phillips Co.: *Richards 2740* (KANU). Rawlins Co.: *McGregor 9470* (KANU). Republic Co.: *Morley 241* (KANU, UC). Rice Co.: *Richards 877* (KANU). Riley Co.: *Gayle 526* (NY). Rooks Co.: *Horr 4987* (KANU). Rush Co.: *Lathrop 3845* (F, KANU, NY). Russell Co.: *Richards 1075* (KANU). Scott Co.: *Gates 16692* (MO). Sedgwick Co.: *Poole 217* (GH). Seward Co.: *Rydberg & Imler 866* (KANU, NY). Sheridan Co.: *Richards 1069* (KANU). Smith Co.: *Richards 2888* (KANU). Stafford Co.: *Richards 875* (KANU). Stanton Co.: *Richards 861* (KANU). Trego Co.: *Richards 1073* (KANU). Wallace

Co.: *Letterman* (MO). Washington Co.: *Horr 4620* (GH, KANU). Wichita Co.: *Agrelius & Agrelius*, in 1912 (KANU). Wilson Co.: *McGregor 14374* (KANU). Woodson Co.: *Richards 603* (KANU). Wyandotte Co.: *Isely 2604* (NY, UC). MASSACHUSETTS: Middlesex Co.: *Jenks*, in 1922 (GH). MICHIGAN: Wayne Co.: *dePaul* (KANU). MINNESOTA: Big Stone Co.: *Gleason 9405* (NY). Chippewa Co.: *Moyer*, in 1897 (ARIZ, UC). Clay Co.: *Dewart* (MO). Goodhue Co.: *Sandberg 566* (F, US). Hennepin Co.: *Aiton*, in 1892 (F, GH, NY, UC). Murray Co.: *Richards 1287* (KANU). Otter Tail Co.: *Chandonnet*, in 1911 (GH). Pipestone Co.: *Anderson*, in 1937 (UC). Polk Co.: *Johnson 520* (GH, NY). Pope Co.: *Taylor*, in 1891 (UC). Rock Co.: *Richards 1296* (KANU). Traverse Co.: *Sheldon*, in 1893 (GH, MO, UC, US). Washington Co.: *Churchill* (NEB). MISSOURI: Greene Co.: *Standley 1533* (US). Jackson Co.: *Bush 163* (MO, OKL, NY, UC, US). Jasper Co.: *Palmer 23389* (GH, NY). Lincoln Co.: *Davis 1390* (MO). Taney Co.: *Steyermark*, in 1938 (F). MONTANA: Broadwater Co.: *Hermann 12323* (US). Cascade Co.: *Cantrell*, in 1947 (OKL). Dawson Co.: *Ward*, in 1883 (US). Gallatin Co.: *Blankinship 283* (F, KANU, MO, US). Jefferson Co.: *Cronquist 6778* (NY). Lewis & Clark Co.: *Kelsey*, in 1888 (F, US). Madison Co.: *Booth*, in 1941 (KANU). Mineral Co.: *Cronquist 6739* (KANU, NY, TAES, TEX). Missoula Co.: *Barkley 1686* (MO, UC). Park Co.: *Scheuber 56* (NY). Rosebud Co.: *Bennett*, in 1957 (F, UC). Sheridan Co.: *Larsen 112* (GH, MO). Stillwater Co.: *Swingle* (CS). Sweetgrass Co.: *Hitchcock & Muhlick 13310* (GH, MO, NY, UC). Wheatland Co.: *Spragg 498* (CS). Yellowstone Co.: *House 4904* (US). NEBRASKA: Adams Co.: *Pammel 232* (MO). Antelope Co.: *Webber 6087* (NEB). Blaine Co.: *Richards 1019* (KANU). Box Butte Co.: *Williamson* (NEB). Brown Co.: *Weinard* (NEB). Buffalo Co.: *Richards 1014* (KANU). Butler Co.: *Cleburne* (NEB). Cass Co.: *Morrison 1187* (MO, NEB). Cedar Co.: *Clements 2a44* (US). Cherry Co.: *Tolstead 450* (GH, NEB). Custer Co.: *Richards 1016* (KANU). Dawes Co.: *Webber 6201* (NEB). Dodge Co.: *Engberg* (NEB). Douglas Co.: *Benke 4314* (F, US). Franklin Co.: *Bates 2955* (NEB). Frontier Co.: *Richards 1028* (KANU). Furnas Co.: *Davidson, Dixit & Romberg 4678* (NEB, OKL). Gage Co.: *Washburn*, in 1899 (US). Hall Co.: *Richards 1012* (KANU). Hamilton Co.: *Richards 1010* (KANU). Jefferson Co.: *Rohbraugh 11* (OKL). Kearney Co.: *Hapeman*, in 1893 (US). Keith Co.: *Werner* (NEB). Keya Paha Co.: *Lawton 35* (F). Kimball Co.: *Moldenke 7228* (NY). Knox Co.: *Wilcox*, in 1888 (NY). Lancaster Co.: *Webber 6090* (MO, NEB). Lincoln Co.: *Richards 1026* (KANU). Logan Co.: *Richards 1022* (KANU). Morrill Co.: *Bates* (NEB). Nance Co.: *Osborn 1136R* (MO). Pierce Co.: *Harms 582* (KANU). Polk Co.: *Turrell* (ARIZ). Red Willow Co.: *Richards 1029* (KANU). Saunders Co.: *Williams 296* (US). Scotts Bluff Co.: *Rydberg 182* (NEB, NY). Sheridan Co.: *Sandoz 172* (NEB). Sioux Co.: *Woods*

354 (NEB). Thomas Co.: *Richards 1021* (KANU). Webster Co.: *Bates* (NEB). York Co.: *Sperry* (TAES). NEW JERSEY: Hudson Co.: *VanSickle*, in 1895 (US). NEW MEXICO: Catron Co.: Eggleston *20242* (US). Colfax Co.: *Lucas 194* (TEX, UC). Curry Co.: *Clark 15241* (UNM). Eddy Co.: *Grassl 88* (F). Guadalupe Co.: *Richards 1110* (KANU). Harding Co.: *Sands* (UNM). Lincoln Co.: *Wooton 261* (MO). Mora Co.: *Richards 3774* (KANU). Otero Co.: *Richards 1121* (KANU). Quay Co.: *Richards 1108* (KANU). Sandoval Co.: *Ellis 207* (US). San Miguel Co.: *Richards 1114* (KANU). Santa Fe Co.: *Standley 5279* (MO). Taos Co.: *Marcelline 2864* (F). Union Co.: *Clark 16179* (UNM). NORTH DAKOTA: Barnes Co.: *Barber 154* (GH). Benson Co.: *Rider 452* (F). Cass Co.: *Alexander* (UC). Grand Forks Co.: *Brannon 213* (MO). Grant Co.: *Bell 604* (UC). Kidder Co.: *Rollins & Munoz 2811* (GH, US). McLean Co.: *Rudd* (OKL). Morton Co.: *Sarvis 99* (US). Richland Co.: *Metcalf 176* (GH). Stutsman Co.: *Mearns 167* (US). Ward Co.: *Larsen 187* (MO, NY). Williams Co.: *Bell 112* (UC). OKLAHOMA: Bryan Co.: *Taylor, Silver & Fox 1230* (OKL). Caddo Co.: *Graber 63* (OKL). Canadian Co.: *Taylor 263* (OKL). Carter Co.: *Richards 543* (KANU). Cherokee Co.: *Wallis 1402* (UC). Cimarron Co.: *Rogers 4664* (US). Cleveland Co.: *Eskew 1007* (MO, OKL). Comanche Co.: *Demaree 13136* (MO, NY, OKL). Cotton Co.: *Waterfall 7277* (OKL). Craig Co.: *Richards 1145* (KANU). Creek Co.: *Bush 307* (MO). Custer Co.: *Mericle 460* (OKL). Dewey Co.: *Richards 3751* (KANU). Ellis Co.: *Richards 1096* (KANU). Garfield Co.: *Richards 1091* (KANU). Garvin Co.: *Richards 536* (KANU). Grady Co.: *Warner 30* (OKL). Grant Co.: *Richards 1090* (KANU). Greer Co.: *Bull*, in 1928 (OKL). Harmon Co.: *Stevens 1079* (GH). Harper Co.: *Stratton 399* (MO). Hughes Co.: *McGregor 13897* (KANU). Johnston Co.: *Alder*, in 1950 (OKL). Kay Co.: *Richards 1088* (KANU). Kingfisher Co.: *Blankinship* (GH, MO, US). Latimer Co.: *McGregor 13894* (KANU). Logan Co.: *Keyser 6014* (NY, OKL). Love Co.: *Richards 545* (KANU). Major Co.: *Richards 1094* (KANU). Marshall Co.: *Duff 93* (ARIZ). McClain Co.: *Hopkins 13355* (OKL). McCurtain Co.: *Poole 15* (KANU). McIntosh Co.: *McGregor 14346* (KANU). Murray Co.: *Richards 540* (KANU). Muskogee Co.: *Bebb 4437* (GH, OKL). Noble Co.: *McGregor 13914* (KANU). Nowata Co.: *Richards 1143* (KANU). Oklahoma Co.: *Waterfall 1397* (NY, OKL). Osage Co.: *Stevens 1952* (GH). Payne Co.: *McLean 132* (ARIZ). Pittsburg Co.: *McGregor 13896* (KANU). Pontotoc Co.: *Richards 535* (KANU). Pottawatomie Co.: *Faulkner 131* (OKL). Roger Mills Co.: *Engleman 1630* (OKL). Rogers Co.: *Hubricht, Shoop & Heinze 1485* (MO). Seminole Co.: *Robbins 3082* (OKL, TAES, UC). Texas Co.: *Harms 1971* (KANU). Tillman Co.: *Fleming 120* (OKL). Tulsa Co.: *Richards 3723* (KANU). Washington Co.: *Richards 3722* (KANU). Woods Co.: *Stevens 764* (GH, MO, OKL, US). Woodward

Co.: *Locke 32* (US). SOUTH DAKOTA: Brookings Co.: *Thornber*, in 1893 (ARIZ, MO). Custer Co.: *Rydberg 802* (NEB, US). Day Co.: *Brenckle 39-78* (NY, US). Fall River Co.: *Hayward 517* (F). Harding Co.: *Visher 374* (F). Hutchinson Co.: *Richards 1302* (KANU). Jackson Co.: *Palmer 37623* (GH, MO, NY). Kingsbury Co.: *Thornber*, in 1894 (GH, MO). Lawrence Co.: *Carr 93* (F, NEB, NY, US). McCook Co.: *Richards 1301* (KANU). Meade Co.: *Forwood 218* (US). Minnehaha Co.: *Richards 1298* (KANU). Pennington Co.: *Visher*, in 1908 (F). Roberts Co.: *Powell*, in 1903 (GH). Spink Co.: *Ricksecker 44* (UC). Turner Co.: *Johnson 77* (GH, MO, NY). Washabaugh Co.: *Visher 2033* (F). Yankton Co.: *Richards 1303* (KANU). TEXAS: Aransas Co.: *Uzzell 37* (LL). Armstrong Co.: *Reverchon 3339* (MO). Bell Co.: *Wolff 892* (TAES, US). Bexar Co.: *Groth 95* (F, GH). Brazoria Co.: *Correll & Edwin 16450* (LL). Brewster Co.: *Mueller 8216* (GH, MO, NY, TEX). Cameron Co.: *Runyon 2638* (F, US). Childress Co.: *Blake 7399* (TEX). Collinsworth Co.: *Correll & Johnston 16901* (LL). Crockett Co.: *Warnock 15176* (LL). Culberson Co.: *Moore & Steyermark 3618* (GH, MO, NY, UC, US). Dallam Co.: *Gorder 116* (LL, TEX). Dallas Co.: *Reverchon 493* (F). Eastland Co.: *Ruth 1314* (NY). Erath Co.: *Gould 5615* (ARIZ, TAES). Galveston Co.: *Traverse 1651* (TEX). Gillespie Co.: *Jermy* (MO). Gray Co.: *Richards 1104* (KANU). Hall Co.: *Fairview School 6515* (TEX). Harris Co.: *Reverchon 3987* (MO). Hartley Co.: *Cory & Parks 16466* (TAES). Hemphill Co.: *Richards 1100* (KANU). Hutchinson Co.: *Thornton 52-430* (TEX). Jeff Davis Co.: *Moore & Steyermark 3133* (GH, MO, NY). Karnes Co.: *Richards 561* (KANU). Kaufman Co.: *Reverchon 3337* (MO). Kenedy Co.: *Tharp 49090* (F). Kent Co.: *Tracy & Earle 369* (MO, NEB). Kerr Co.: *Heller 1850* (ARIZ, GH, MO, NY, UC, US). Lipscomb Co.: *Richards 1097* (KANU). Lubbock Co.: *Demaree 7706* (GH, MO). Matagorda Co.: *Cory 20290* (GH). McLennan Co.: *Smith 865* (TEX). Medina Co.: *Richards 3746* (KANU). Menard Co.: *Cory* (TAES). Moore Co.: *Jespersen 2704* (F, MO, NY, UC, US). Nueces Co.: *Heller 1789* (TEX). Ochiltree Co.: *Wallis 7198* (TEX). Oldham Co.: *Richards 1106* (KANU). Parker Co.: *Ruth 1314* (US). Pecos Co.: *Tharp 43-938* (OKL, TEX, UC). Potter Co.: *Palmer 12535* (MO, UC). Presidio Co.: *Hinckley 656* (F). Randall Co.: *Palmer 13878* (MO, US). Reeves Co.: *Gillespie 5253* (UC). Roberts Co.: *Richards 1102* (KANU). Robertson Co.: *Marsh & Calley 74* (TEX). Sherman Co.: *Jackson 5* (KANU). Smith Co.: *Reverchon 2229* (MO). Stephens Co.: *Denton*, in 1931 (TEX.) Sutton Co.: *Gould 5729* (TAES, TEX, UC). Tarrant Co.: *Reverchon 1435* (F, GH, KANU, NEB, NY). Taylor Co.: *Tracy 7891* (F, GH, MO, NEB, NY, TEX, US). Terrell Co.: *Palmer 33538* (NY). Tom Green Co.: *Tweedy 297* (US). Travis Co.: *Barkley 13321* (TEX). Uvalde Co.: *Kincaid & Johnston 54637* (TEX). Val Verde Co.: *Jones 25903* (MO). Victoria Co.: *Richards 3736* (KANU). Williamson

Co.: *York 46218* (NEB, TAES, TEX). Wise Co.: *Shinners 7930* (UC). Young Co.: *Gentry 1254* (TEX). UTAH: Cache Co.: *Holmgren 3752* (GH, NY, UC, US). WISCONSIN: Milwaukee Co.: *Shinners 2342* (GH, UC). Sauk Co.: *Steele 72* (US). Walworth Co.: *Wadmond L.9 16211* (GH, LL). WYOMING: Albany Co.: *Goodman 776* (MO, OKL). Campbell Co.: *Porter & Porter 7568* (UC). Carbon Co.: *Hanna 1053* (MO). Converse Co.: *Porter 3151* (GH, MO, UC). Crook Co.: *Hayward 210* (F). Hot Springs Co.: *Mulford*, in 1892 (GH, MO). Johnson Co.: *Tweedy 3143* (NY). Laramie Co.: *Pammel*, in 1913 (GH). Niobrara Co.: *Harms 2131* (KANU). Park Co.: *Witt 1385* (NY). Platte Co.: *Nelson 386* (GH, MO, NY, US). Sheridan Co.: *Rollins 556* (NY). CANADA: ALBERTA: *Moodie 1181* (F, GH, NY, UC, US). BRITISH COLUMBIA: *Shaw 1143* (GH, MO, NEB, NY, US). MANITOBA: *Dawson*, in 1873 (GH). ONTARIO: *Dodge*, in 1911 (MO, TEX). SASKATCHEWAN: *Macoun 5068* (GH, US). MEXICO: COAHUILA: *Palmer 345* (F, GH, MO, NY, US). HIDALGO: *Chase 7117* (F, GH, MO, NY). NUEVO LEON: *Taylor 27* (F, MO, TEX). SAN LUIS POTOSI: *Lundell 5103* (ARIZ, MO, US). TAMAULIPAS: *Tracy 8947a* (NEB). VERA CRUZ: Det. by Hoffman *213* (GH).

4b. *R. COLUMNIFERA* (Nutt.) Woot. & Standl. forma *PULCHERRIMA* (DC.) Fernald, Rhodora **40**:353. 1938.

Obeliscaria pulcherrima DC., Prodr. 5:559. 1836.

Obeliscaria columnaris DC. var. *pulcherrima* (DC.) D. Don, Sweet's Brit. Fl. Gard. Ser. 2, **4**:361. 1838.

Lepachys columnaris Torr. & Gray var. *pulcherrima* (DC.) Torr. & Gray, Flora N. Am. 2:315. 1842.

Ratibida columnifera (Nutt.) Woot. & Standl. var. *pulcherrima* (DC.) Woot. & Standl., Contrib. U. S. Nat. Herb. **19**:706. 1915.

Lepachys columnifera (Nutt.) Rydb. var. *pulcherrima* (DC.) Rydb., Flora Prairies and Plains of Central North America, 838 p. 1932.

Ratibida columnaris (Sims) D. Don forma *pulcherrima* (DC.) Sharp, Ann. Mo. Bot. Gard. **22**:70-71. 1935.

Differs from *R. columnifera* only by the purplish-yellow to purple ray flowers. (Figs. 6 and 9).

Flowering time. March-November.

Lectotype. Texas: Mexican province. San Fernando to Bejar, June, 1832, *Berlandier 1960* (G-DC?, Microfiche!; Isotype GH!). Since deCandolle did not select a type from

Plate 1392

Fig. 6. *Ratibida columnifera* f. *pulcherrima*. ca. 1/3 actual size. *Richards 567* (KANU).

the original material, the above lectotype was selected by the author.

Habitat and Distribution. Prairies, foothills, and mountains of Canada, United States, and Mexico.

Ratibida columnifera f. *pulcherrima* is characterized by having showy, purplish-yellow to purple ligules. Since deCandolle (1836) first described this as a species, its has attracted attention in nurseries and gardens, and it is invariably collected in the field as being something different. It is recognized as a color form in this work because of its obvious color difference and its distinct distribution pattern. It occurs abundantly in northern Mexico, Texas, and New Mexico and is infrequently found farther north in the prairie and central states as compared to the yellow-liguled plants. Pure populations of the purple forms are common above 7,000 ft. in the Sacramento Mountains of New Mexico with isolated pure purple plants found infrequently over the range of the form.

Representative specimens selected from 842 sheets: UNITED STATES: ARIZONA: Apache Co.: *Griffiths 5382* (US). Gila Co.: *Johnson 1697* (KANU). Navajo Co.: *Thornber 4576* (ARIZ). ARKANSAS: Hempstead Co.: *Palmer 8024* (MO, NY). Lawrence Co.: *Demaree 30991* (KANU, MO). Miller Co.: *Eggert*, in 1898 (MO, NY). COLORADO: Archuleta Co.: *Baker 698* (F, MO, NY, US). Baca Co.: *Harrington & Smith 296* (ARIZ). Denver Co.: *Clokey 2819* (TEX). El Paso Co.: *Durshel 4191* (MO). Jefferson Co.: *Letterman*, in 1913 (MO). Larimer Co.: *Crandall 2980* (ARIZ). Las Animas Co.: *Richards 1130* (KANU). Weld Co.: *Osterhout 2310* (NY). KANSAS: Barber Co.: *Richards 773* (KANU). Cheyenne Co.: *Horr 4685* (GH, KANU). Coffey Co.: *Horr 3467* (KANU). Edwards Co.: *Carleton 308* (US). Ellis Co.: *Crockett 182* (OKL). Decatur Co.: *Richards 2835* (KANU). Grant Co.: *Thompson 15* (GH, MO). Gove Co.: *Kellerman*, in 1893 (KANU). Meade Co.: *McGregor & Horr 4954* (KANU). Morton Co.: *Richards 2967* (KANU). Sheridan Co.: *Richards 1059* (KANU). Sherman Co.: *McGregor 5212* (KANU). MISSOURI: Jackson Co.: *Bush 4019* (NY). MONTANA: Cascade Co.: *Safford 591* (US). Dawson Co.: *Ward*, in 1883 (US). Meagher Co.: *Anderson 232* (MO). Rosebud Co.: *Bennett*, in 1957 (US). NEBRASKA: Banner Co.: *Rydberg* (NEB). Box Butte Co.: *Williamson* (NEB). Buffalo Co.: *Richards 1013* (KANU). Cedar Co.: *Clements 2644* (NEB). Custer Co.: *Richards 1018* (KANU). Dawes Co.: *Webber 6200* (MO, NEB). Dawson Co.: *Bates* (NEB). Franklin Co.: *Laybourn 79* (MO).

Hooker Co.: *Rydberg 1445* (NEB, US). Kearney Co.: *Hapeman,* in 1893 (ARIZ, US). Lancaster Co.: *Hedgcock,* in 1899 (MO). Lincoln Co.: *Richards 1024* (KANU). Morrill Co.: *Bates* (NEB). Rock Co.: *Bates,* in 1896 (GH). Scotts Bluff Co.: *Rydberg 183* (NEB, NY). Sheridan Co.: *Hatcher,* in 1886 (NY). Sioux Co.: *Woods 353* (NEB). Thomas Co.: *Richards 1020* (KANU). Webster Co.: *Bates* (NEB). NEW MEXICO: Bernalillo Co.: *Jackson 2085* (UNM). Catron Co.: *Eggleston 20388* (NY). Chaves Co.: *Earle & Earle,* in 1900 (NY). Colfax Co.: *Richards 1128* (KANU). Curry Co.: *Reynolds 243* (UNM). Eddy Co.: *Grassl 88* (GH). Grant Co.: *Jones* (UNM). Guadalupe Co.: *Richards 1109* (KANU). Harding Co.: *Sands* (UNM). Lea Co.: *Castetter 9003* (UNM). Lincoln Co.: *Wooton 247* (GH, MO, NY, UC, US). Otero Co.: *Richards 1122* (KANU). Quay Co.: *Fisher 56* (MO, US). Rio Arriba Co.: *Standley 6762* (US). Sandoval Co.: *Hershey* (UNM). San Miguel Co.: *Richards 1125* (KANU). Sante Fe Co.: *Arsene 15909* (UC). Socorro Co.: *Metcalfe 415* (ARIZ, GH, MO, NY, UC, US). Taos Co.: *Dixon A-370* (UNM). Torrance Co.: *Jackson 2166* (UNM). Valencia Co.: *Jones 122* (UNM). NORTH CAROLINA: Moore Co.: *Pinehurst Nurseries,* in 1902 (MO). NORTH DAKOTA: Benson Co.: *Lunell,* in 1917 (MO, US). Grand Forks Co.: *Churchill* (NEB). McKenzie Co.: *Stevens 727* (MO, UC). Stark Co.: *Mearns 168* (US). Steele Co.: *Stevens,* in 1949 (US). Ward Co.: *Larsen 194* (MO, NY, US). Wells Co.: *Bolley,* in 1891 (NY). OKLAHOMA: Beckham Co.: *Mericle 378* (OKL). Cimarron Co.: *Waterfall 7441* (OKL). Cleveland Co.: *Myers 49* (OKL). Comanche Co.: *McCurry 1190* (OKL). Mayes Co.: *Wallis 7676* (KANU, OKL, TEX). McCurtain Co.: *Wehling 24* (OKL). Payne Co.: *Waugh 260* (US). Tillman Co.: *Duncan 28* (MO). SOUTH DAKOTA: Brookings Co.: *Thornber* (ARIZ). Custer Co.: *Murdoch* (F). Hutchinson Co.: *Harms 554* (KANU). Kingsbury Co.: *Thornber,* in 1892 (MO, UC). Meade Co.: *Forwood 218a* (US). Moody Co.: *Ball & Ball 882* (US). Spink Co.: *Ricksecker 45* (UC). Washabaugh Co.: *Visher 2033* (NY). TENNESSEE: Davidson Co.: *Gattinger,* in 1886 (F, MO, NY). TEXAS: Anderson Co.: *Eggert,* in 1899 (MO). Andrews Co.: *Scudday* (LL). Aransas Co.: *Richards 3738* (KANU). Armstrong Co.: *Reverchon 494* (MO). Bailey Co.: *Correll 13102* (LL). Bastrop Co.: *Richards 3725* (KANU). Bee Co.: *Richards 559* (KANU). Bell Co.: *York & York B44* (TEX). Bexar Co.: *Richards 568* (KANU). Brazoria Co.: *Correll & Edwin 16451* (LL). Brazos Co.: *Palmer 7792* (MO, NY). Brewster Co.: *Tharp 8833* (TEX). Caldwell Co.: *Richards 550* (KANU). Cameron Co.: *Traverse 1015* (F, LL, MO, TEX, US). Childress Co.: *Childress Biological Class,* in 1930 (MO). Comal Co.: *Lindheimer 642* (MO). Crane Co.: *Warnock 14697* (LL, TEX). Crockett Co.: *Degener 5093* (NY). Culberson Co.: *Shreve 8121* (ARIZ). Dewitt Co.: *Richards 554* (KANU). Dickens Co.: *Graham 8* (TEX). Eastland Co.: *Hodge Oak Park School 50* (TEX). Edwards Co.: *Gould 6810* (TAES). Erath

Co.: *Hoisington 88* (OKL, TEX, UC). Galveston Co.: *Reverchon 3987* (NY). Garza Co.: *Ruth 1313* (US). Gillespie Co.: *Richards 3747* (KANU). Goliad Co.: *Richards 558* (KANU). Gonzales Co.: *Richards 551* (KANU). Gray Co.: *Stemen 122* (OKL). Grayson Co.: *Richards 3724* (KANU). Gregg Co.: *Eggert,* in 1899 (MO). Guadalupe Co.: *Richards 567* (KANU). Hall Co.: *Reverchon,* in 1904 (MO). Harris Co.: *Traverse 1492* (F, LL). Hays Co.: *Walker 44* (TEX). Hemphill Co.: *Eggert,* in 1900 (MO). Hidalgo Co.: *Tracy 8923* (F, GH, MO, NEB, NY, TAES, TEX, US). Howard Co.: *Correll 16340* (LL). Jackson Co.: *Drushel 9564* (US). Jeff Davis Co.: *Waterfall 4730* (GH, MO, NY). Karnes Co.: *Richards 560* (KANU). Kenedy Co.: *Johnston 53.280.85* (TAES, TEX). Kent Co.: *Tracy & Earle 369* (TEX). Kerr Co.: *Perdue 1597* (LL, UC). Kinney Co.: *Mearns 1467* (US). Kleberg Co.: *Cory 51294* (GH, NY, TAES, US). Lamar Co.: *Shinners 7864* (GH). La Salle Co.: *Mauermann 22* (TEX). Llano Co.: *Parks & Cory 6310* (TAES). Lubbock Co.: *Demaree 7675* (GH, LL, MO, US). Martin Co.: *Eggert,* in 1900 (MO). Mason Co.: *Taylor* (TAES). Matagorda Co.: *Beamer,* in 1953 (KANU). Maverick Co.: *Bray* (TEX). McMullen Co.: *Thompson & Graham 67* (TEX). Medina Co.: *Shinners 7302* (GH). Midland Co.: *Tracy 7881* (F, GH, MO, NEB, NY, TEX). Nueces Co.: *Pennell 10341* (NY). Oldham Co.: *Hubricht A1435* (MO). Parmer Co.: *Shinners 8332* (GH). Pecos Co.: *Warnock 11845* (LL). Potter Co.: *Richards 1105* (KANU). Presidio Co.: *York 48101* (KANU, TAES, TEX). Randall Co.: *Eggert,* in 1901 (MO). San Patricio Co.: *Richards 3740* (KANU). Scurry Co.: *Harris,* in 1927 (TEX). Smith Co.: *Moore 828* (GH). Starr Co.: *Tharp & Johnston 541899A* (TEX). Sutton Co.: *Aldwell Bros. 17499* (TAES). Tarrant Co.: *Ruth 1054* (GH). Taylor Co.: *Tolstead 7274* (GH, MO, NEB, NY, TEX). Terrell Co.: *Webster 255* (TEX). Tom Green Co.: *Smith 16* (GH, OKL). Travis Co.: *Richards 549* (KANU). Val Verde Co.: *Jones 25904* (MO, UC). Victoria Co.: *Richards 556* (KANU). Washington Co.: *Brackett 285* (GH, TEX). Webb Co.: *Orcutt 5768* (MO). Wharton Co.: *Drushel 10723* (NY). Willacy Co.: *Johnston 53.280.87* (TEX). Williamson Co.: *York 46218* (OKL). Wilson Co.: *Richards 563* (KANU). Zapata Co.: *Clover 699* (US). UTAH: Grand Co.: *Holmgren & Hansen 3496* (GH, NY, US). WYOMING: Converse Co.: *Nelson 8416* (ARIZ). Laramie Co.: *Shantz* (NEB). Natrona Co.: *Nelson 570* (MO, NY, UC, US). CANADA: ALBERTA: *Moodie 1188* (NY, US). MANITOBA: *Macoun 12243* (NY). MEXICO: CHIHUAHUA: *Shreve 7979* (ARIZ). COAHUILA: *Nelson 6152* (F, US). NUEVO LEON: *Frye & Frye 2358* (ARIZ, GH, MO, NY, UC). TAMAULIPAS: *Tracy 8947a* (F, GH, MO, NY, TAES, TEX).

5. *RATIBIDA LATIPALEARIS* Richards, Rhodora **66** (767):267, 268. 1964.

Plate 1393

Fig. 7. *Ratibida latipalearis.* ca. 1/3 actual size. *Richards 3770* (KANU).

Stems one or more, branched, sulcate, 5.5-11.7 dm high, strigose-hirsute, unicellular globular glands interspersed in the grooves, average number of ridges 10 just below inflorescence. Leaves strigose-hirsute, punctate on both surfaces, basal leaves long petioled, 3.2-26.5 cm long, ovate-obovate, crenate to 3-7 pinnately cleft, 3-nerved, lateral segments entire to serrate-crenate, oblong-oblanceolate, 0.2-4.0 cm long, 0.2-2.4 cm wide, terminal lobe ovate, serrate-crenate to cleft-parted, 2.0-7.0 cm long, 0.2-3.6 cm wide, upper leaves ovate-obovate or oblong, 2.7-14.3 cm long, 1.9-8.5 cm wide, 3-9 pinnate or pinnately cleft, terminal segment lanceolate, parted or cleft, 2.0-7.0 cm long, 0.6-4.5 cm wide, lateral segments oblanceolate, entire or cleft, 0.2-4.7 cm long, 0.1-1.5 cm wide. Peduncles 11.8-33.5 cm long. Heads solitary, columnar, 1.7-3.5 cm long, 0.9-1.3 cm wide, on naked peduncles; receptacles linear, 1.7-3.3 cm long, 1.2-4.0 mm wide, narrowing to apex. Phyllaries reflexed, 10-12, linear-lanceolate, black punctate glands present, inner suface glabrous except for strigose-hirsute marginal tips, biseriate, outer row 0.6-1.1 cm long, 1.0-1.2 mm wide, inner row 0.3-0.8 cm long, 0.8-1.2 mm wide. Ray flowers 8-17, yellow, lanceolate-oblanceolate, or oval-oblong, 0.8-3.1 cm long, 0.4-1.2 cm wide, outer surface hirsute, black resinous and punctate glands interspersed on outer surface, inner surface glabrous, tube short, 1.0-2.0 mm long, apex 2-3 lobed, lobes 0.2-8.2 mm long, 0.2-3.5 mm wide. Disc corollas dark greenish-yellow, 1.6-2.0 mm long, lobe segments 0.6-1.0 mm wide, apex lobes reflexed, ovate, 0.5-1.0 mm long, black resinous glands present on outer lobe surface; anthers sagittate, 1.2-2.0 mm long, tips with black resinous glands on outer surface, filaments 0.5-1.2 mm long, attached to base of anther; styles 1.0-1.8 mm long, filiform, the branches 2, 0.8-1.2 mm long, stigmatic surface restricted to tip, a fourth the length of the style branch. Palea 2.8-3.0 mm long, 4.0-5.0 mm wide, adaxial side hyaline, winged, ciliate, abaxial side hirsute half way down to base, few unicellular, black glands near base; vertical oblanceolate resin gland present in center of palea 1.0-1.2 mm long. Achenes oblong-oblanceolate, 2.0-3.0 mm long, 1.1-1.4 mm wide, adaxial margin glabrous, occasionally ciliate or with black, stalked glands; pappus 1-2 minute teeth or absent. (Figs. 7, 9, 11f, 12f, 13f).

Flowering time: August-October.

Holotype. Mexico. Chihuahua: Colonia Garcia, 37 miles southwest of Colonia Juarez, pine forest meadow, August 29, 1962, *Richards 3770* (KANU!; Isotypes F!, GH!, KANU!, MO!, NY!, UC!, US!).

Habitat and Distribution. Pine forest meadows, valleys and rocky pine slopes of Sierra Madre Occidental, Chihuahua, Mexico.

Ratibida latipalearis, as presently known, is limited in distribution to Chihuahua, Mexico. It was recognized as a new species because of the non-dissected, triple-nerved, first basal leaves, the greenish-yellow heads with 8-17 upright ligules, black glands on the ligules, phyllaries, petal lobes of the disc corollas and the apex of the anthers, palea mostly broader than long with unicellular black glands from the middle to the base of the adaxial margin, and the branching habit of the stem.

Representative specimens selected from 19 sheets: MEXICO: CHIHUAHUA: *Dobie 2* (TEX); *LeSueur 988* (F, MO, TEX, UC); *Muller 3547* (LL, UC); *Richards 3770* (KANU); *Townsend & Barber 230* (F, MO, NY, UC, US); *Tucker 2573* (ARIZ).

6. *RATIBIDA TAGETES* (James) Barnh., Bull. Torr. Bot. Club 24:410. 1897.

Rudbeckia tagetes James, Long's Exped. 2:68. 1823.

Rudbeckia globosa Nutt., J. Acad. Natur. Sci. Phila. 7:79. 1834.

Obeliscaria tagetes DC., Prodr. 5:559. 1836.

Lepachys columnaris Torr. & Gray var. *tagetes* Gray, Smiths. Contrib. Knowl. (Pl. Wright.) 3:106. 1852.

Lepachys tagetes (James) Gray, Pac. Railw. Report. 4:103. 1856.

Ratibida tagetes (James) Barnh. var. *cinera* Standley, Muhlenb. 5:30. 1909.

Stems one or many, branched, 1.6-5.4 dm tall. Leaves ovate-obovate or linear-oblong, 0.6-8.6 cm long, 0.2-6.6 cm wide, pinnately or bipinnately cleft into 2-7 lobes, narrowly lanceolate, 0.3-4.3 cm long, 0.8-4.0 mm wide, lower leaves are lanceolate and may be entire, a few upper leaves cauline and entire. Peduncles 0.3-6.4 cm long. Heads solitary, globular, 0.6-1.4 cm long, 0.6-1.2 cm wide. Phyllaries 10-12, the inner series ovate, 1.2-3.8 mm long, 0.4-1.5 mm wide, the outer lanceolate, 1.2-6.0 mm long, 0.6-2.4 mm wide. Ray flowers 5-10, yellow, purplish-yellow to purple, oval-oblong, 2.8-8.5 mm long, 2.0-6.0 mm wide, hirsute on outer surface, punctate glands numerous on outer surface, inner surmace glabrous, 2-3 lobed apex, lobes 0.1-2.1 mm long, 0.3-3.0 mm wide. Disc corollas 1.2-1.9 mm long, lobes 0.5-0.8 mm wide, apex punctate, 0.5-1.0 mm long; anthers 1.0-1.5 mm long, punctate glands abundant on outer apex, filaments 0.4-1.0 mm long; styles 1.0-1.9 mm long, the branches 0.8-1.2 mm long, stigmatic portion a fourth the length of the style branch. Palea 2.1-4.0 mm long, 1.5-2.5 mm

Plate 1394

Fig. 8. *Ratibida tagetes.* ca. 1/3 actual size. *Richards 1111* (KANU).

wide, punctate glands at apex, adaxial edge hyaline, ciliate, abaxial edge strigose to below the center, unicellular glands from below center to the base, resin gland linear-oblanceolate, 1.1-2.1 mm long. Achenes oblong-oblique, 1.9-2.8 mm long, 1.2-2.0 mm wide, glabrous except some ciliation at apex, winged adaxial edge; pappus a thick-crowned corona. (Figs. 8, 10, 11c, 12c, 13c).

Flowering time: May-October.

Holotype. Colorado: Otero County, south of La Junta, in prairie near stagnant pool, July 24, 1820, *James* (NY!).

Habitat and Distribution. Prairies, high plains, and rocky hillsides. Colorado, Kansas, Oklahoma, southwestern United States, and Chihuahua, Mexico.

Standley (1909) described *Ratibida tagetes* var. *cinera* (Holotype *Standley 5156* NY!; Isotype MO!, US!) based on the stem and peduncles being cinerous and densely tomentose-hirsute with gray leaves also very densely strigose-hirsute. This is the only known occurrence of Standley's variety but with transplants from Seward County, Kansas (*Richards 3777* KANU), a pubescence similar to the above named variety was observed on greenhouse plants. Further observation led to the discovery of a minute gall or bud mite (Eriophyidae) feeding in the tomentose-hirsute areas. Use of insecticides stopped further outbreak of this phenomenon and the plants recovered, with the exception of small dead portions, to appear normal and flower. Careful study of Standley's type *5156* revealed the remains of similar mite exoskeletons. One other collection of *Ratibida tagetes*, Colfax County, New Mexico, *Lucas 193* (OKL), exhibited this cinerous type of pubescence and again similar mite remains were seen in the areas showing the pubescence of Standley's variety.

In addition to the bud mite, hyphal filaments of a Deuteromycete were seen on a slide made by scraping the leaf surface in the noticeable areas of pubescence from Standley's specimens and staining with lacto-phenol cotton blue. Standley (1909) mentions the possibility that his variety might be the typical form of *R. tagetes* affected by some fungus. On another specimen, *Lucas 193* (OKL), conidia and hyphal filaments of *Alternaria* were seen on a mounted

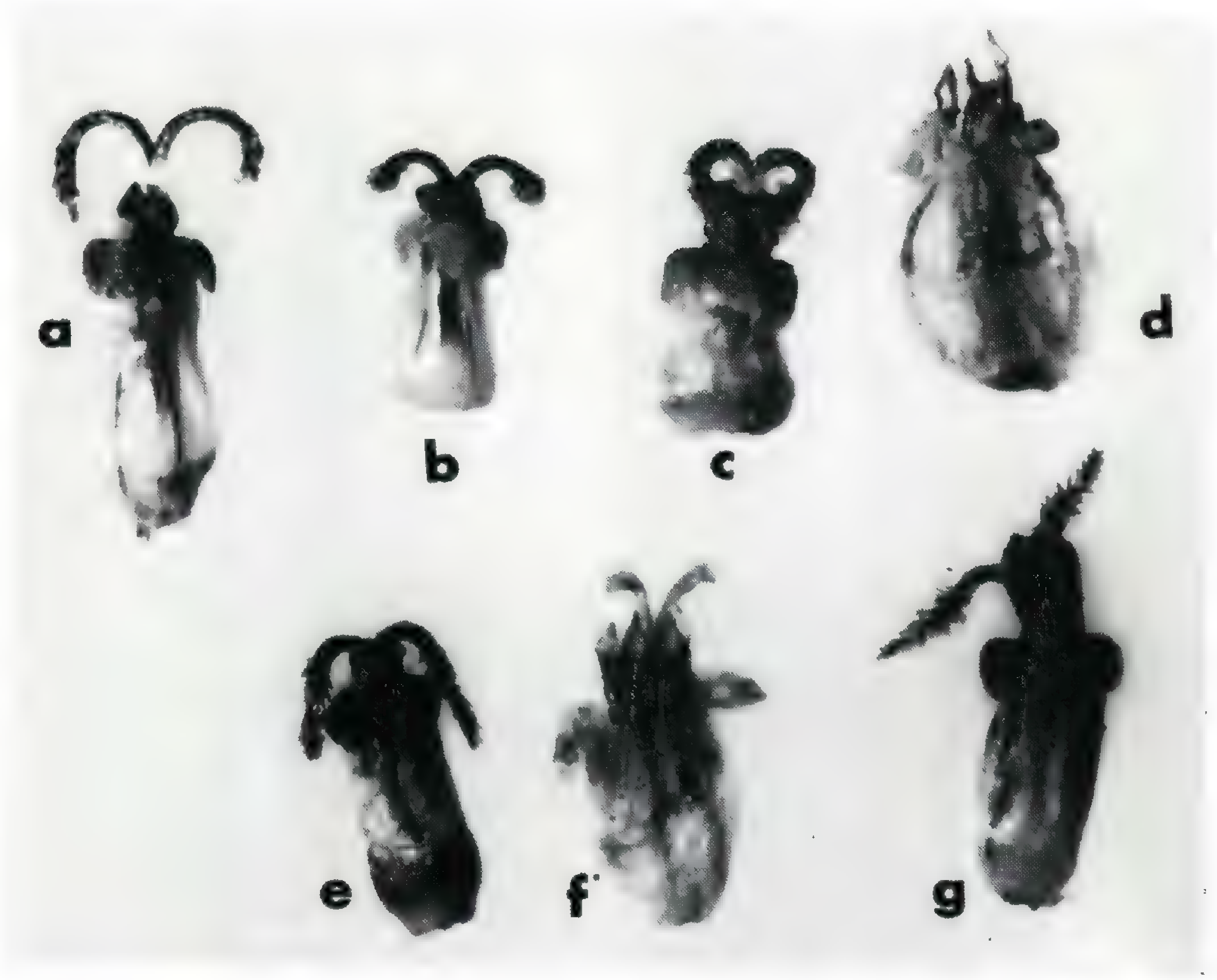

Plate 1395

Fig. 11. Disc Corollas of *Ratibida*; ca. × 9. a. *R. pinnata*; b. *R. columnifera*; c. *R. tagetes*; d. *R. mexicana*; e. *R. peduncularis* var. *picta*; f. *R. latipalearis*; g. *R. peduncularis* var. *peduncularis*.

slide. Conidia and hyphal filaments were also taken from *Richards 3777* (KANU).

The above leads the author to believe that either mites or a fungus or both are the cause of the cinerous pubescence of Standley's variety and it is, therefore, not recognized in this study.

Ratibida tagetes is a short species characterized by small globular heads, narrowly linear or dissected leaves, yellow to purple ligules, and a well-formed tap root which produces adventitious buds from horizontal branches, leading to clonal development. The purple and purplish-yellow ligules have never been recognized as a color form probably because they usually occur together, infrequently being found in pure colonies. The rays are small and inconspicuous com-

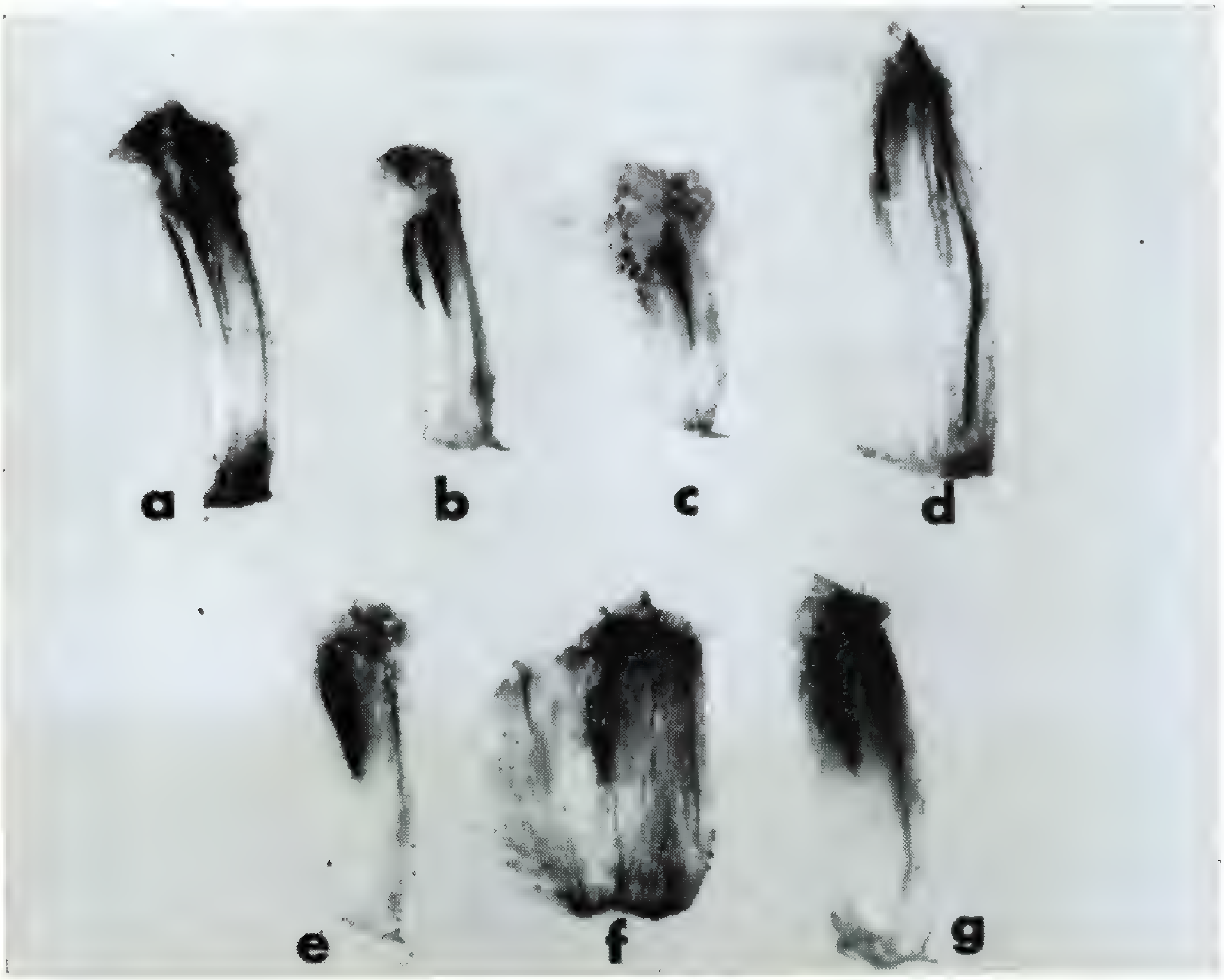

Plate 1396

Fig. 12. Paleae of *Ratibida*; ca. × 9. a. *R. pinnata*; b. *R. columnifera*; c. *R. tagetes*; d. *R. mexicana*; e. *R. peduncularis* var. *picta*; f. *R. latipalearis*; *g. R. peduncularis* var. *peduncularis.*

pared to the larger showy ones of the color form of *R. columnifera.* Wooton and Standley (1915) mention the small rays of *R. tagetes* and the various forms as reasons for not naming a new variety.

Representative specimens selected from 398 sheets: UNITED STATES: ARIZONA: Apache Co.: *Griffiths 5092* (US). Coconino Co.: *Deaver* (ARIZ). COLORADO: Archuleta Co.: *Bethel & Payson*, in 1917 (NY). Baca Co.: *Richards 1132* (KANU). Bent Co.: Coll. unknown *572* (CS). Cheyenne Co.: *Robertson 1474* (CS). Denver Co.: *Engelmann*, in 1874 (MO). Fremont Co.: *Shear 3769* (NY, UC, US). Gunnison Co.: *Baker 667* (GH, MO, NY, UC, US). Huerfano Co.: *Parry 110* (MO). Kit Carson Co.: *Preston* (CS). Las Animas Co.: *Richards 1131* (KANU). Lincoln Co.: *Ownbey 1348* (GH, MO, NY, UC). Otero Co.: *Richards 3776* (KANU). Prowers Co.: *Christ 583* (CS). Pueblo Co.: *Woodward 156* (GH). KANSAS: Barber Co.: *McGregor 14790* (KANU). Edwards Co.: *Richards 3764* (KANU). Finney Co.: *Wilson*

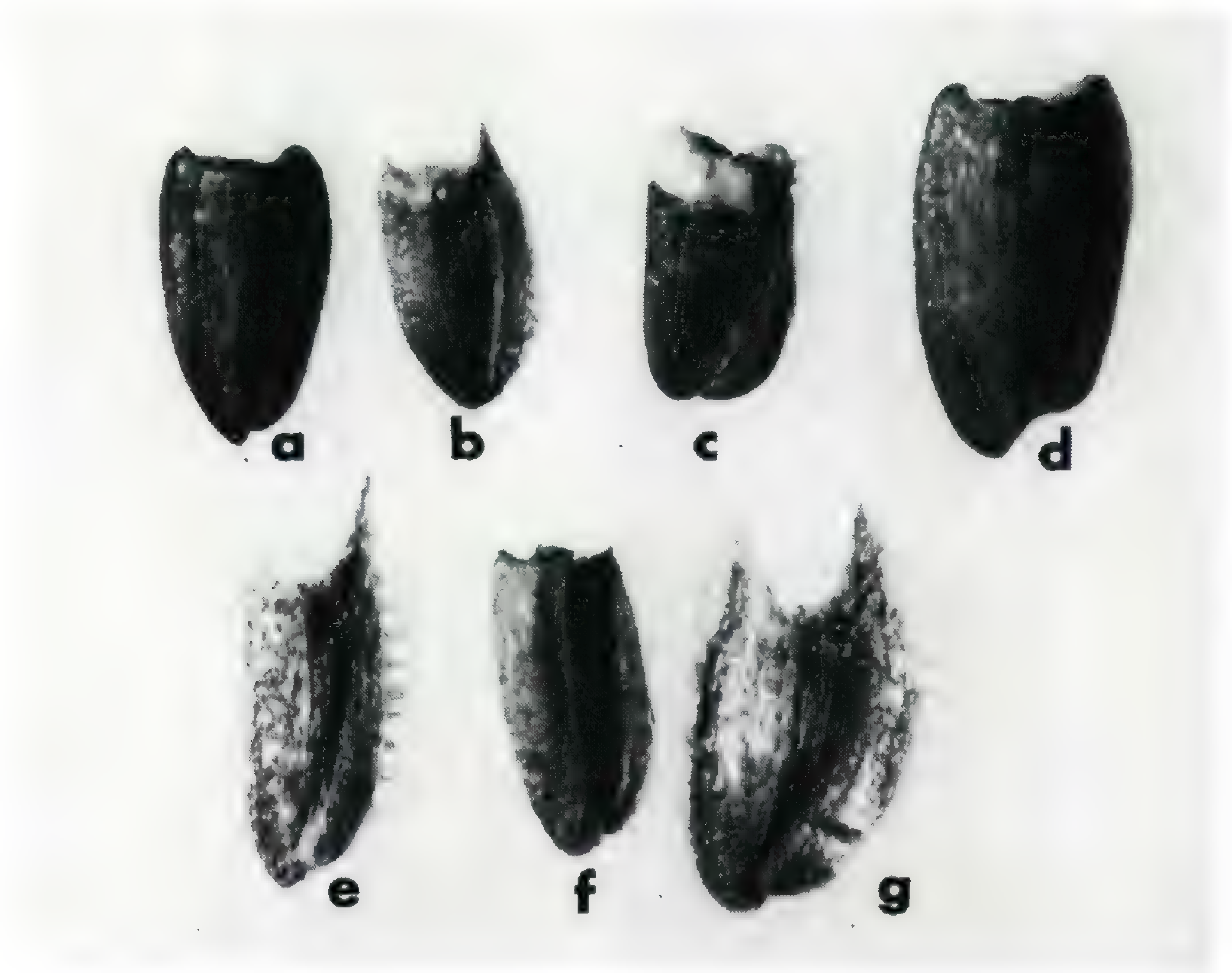

Plate 1397

Fig. 13. Achenes of *Ratibida*; ca. × 10. a. *R. pinnata;* b. *R. columnifera*; c. *R. tagetes*; d. *R. mexicana*; e. *R. peduncularis* var. *picta*; f. *R. latipalearis*; g. *R. peduncularis* var. *peduncularis.*

& *Miller,* in 1912 (KANU). Ford Co.: *Richards 3762* (KANU). Grant Co.: *McGregor 13993* (KANU). Gray Co.: *McGregor 15773* (KANU). Greeley Co.: *Reed,* in 1892 (MO, UC, US). Hamilton Co.: *Rydberg & Imler 1017* (KANU, NY). Kearney Co.: *Rydberg & Imler 938* (KANU, NEB, NY). Logan Co.: *McGregor 17245* (KANU). Meade Co.: *Richards 3759* (KANU). Morton Co.: *Richards 3570* (KANU). Russell Co.: *Hitchcock 268* (GH, KANU, MO, NY, US). Scott Co.: *Agrelius, Wilson & Agrelius,* in 1912 (KANU). Seward Co.: *Richards 3761* (KANU). Sherman Co.: *Harshbarger 3801* (US). Stanton Co.: *Thompson 68* (F, MO, NY, UC, US). Stevens Co.: *Harms 752* (KANU). Trego Co.: *Bodin 20* (F). Wallace Co.: *Letterman,* in 1884 (MO, NY). NEW MEXICO: Bernalillo Co.: *Jones 4118* (F, US). Colfax Co.: *Richards 1129* (KANU). Dona Ana Co.: *Wooton 5* (GH, MO, NY, US). Eddy Co.: *Standley 40347* (US). Grant Co.: *Bigelow 5571* (NY). Guadalupe Co.: *Richards 1111* (KANU). Hidalgo Co.: *Wolf 2591* (GH). Lea Co.: *Harms 1786* (KANU). Lincoln Co.: *Skehan 32* (F, GH, MO, NY, UC, US). McKinley Co.: *Dittmer 9020* (UNM). Mora Co.:

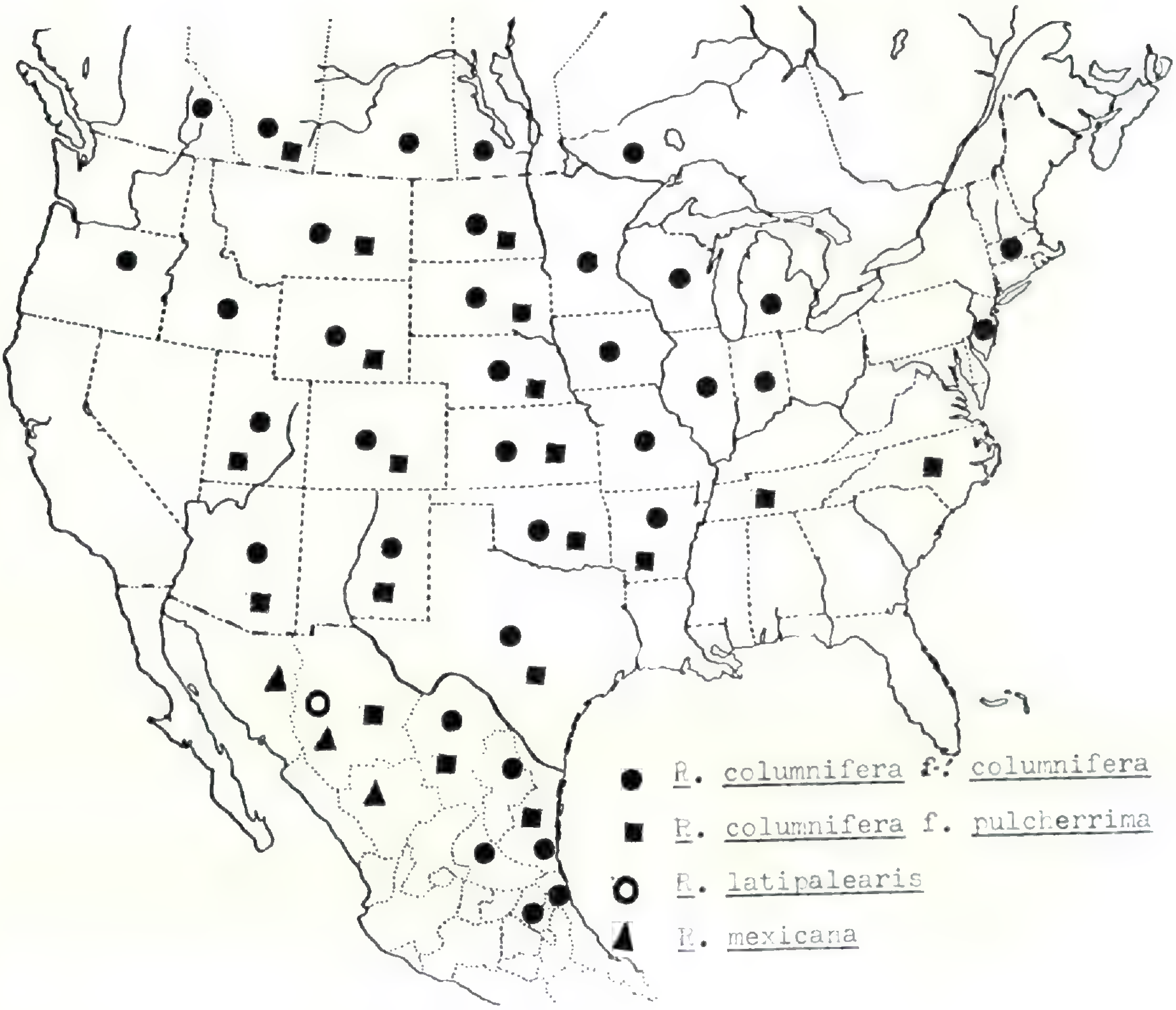

Fig. 9. Distribution of *Ratibida*.

Richards 3773 (KANU). Quay Co.: *Fisher 157* (US). Rio Arriba Co.: *Jackson 2511* (UNM). Roosevelt Co.: *Dittmer 9018* (UNM). Sandoval Co.: *Ellis 208* (US). San Miguel Co.: *Richards 3772* (KANU). Santa Fe Co.: *Heller & Heller 3829* (ARIZ, GH, KANU, MO, NEB, NY, US). Sierra Co.: *Jackson 2814* (KANU). Socorro Co.: *Dunn 5281* (UNM). Torrance Co.: *Clark 10328* (UNM). Union Co.: *Harms 1958* (KANU). Valencia Co.: *Dittmer 9019* (UNM). OKLAHOMA: Cimarron Co.: *Demaree 13301* (GH, NY, OKL). Harmon Co.: *Stevens 1080* (GH, MO, NY, OKL). Texas Co.: *Williams 95* (UC). TEXAS: Brewster Co.: *Warnock W919* (GH, TEX). Crane Co.: *Tharp*, in 1941 (TEX). Crockett Co.: *Parks & Cory 29672* (TAES). Culberson Co.: *Tharp & Janszen 49-1002* (TEX). Dallam Co.: *Griffiths 5641* (MO, US). Deaf Smith Co.: *Shinners 8334* (TEX). El Paso Co.: *Waterfall 3956* (ARIZ, GH, MO). Hartley Co.: *Palmer 14142* (MO, US). Hudspeth Co.: *Mulford 260* (MO, NY). Lamb Co.: *Shinners 8354* (GH, UC). Lub-

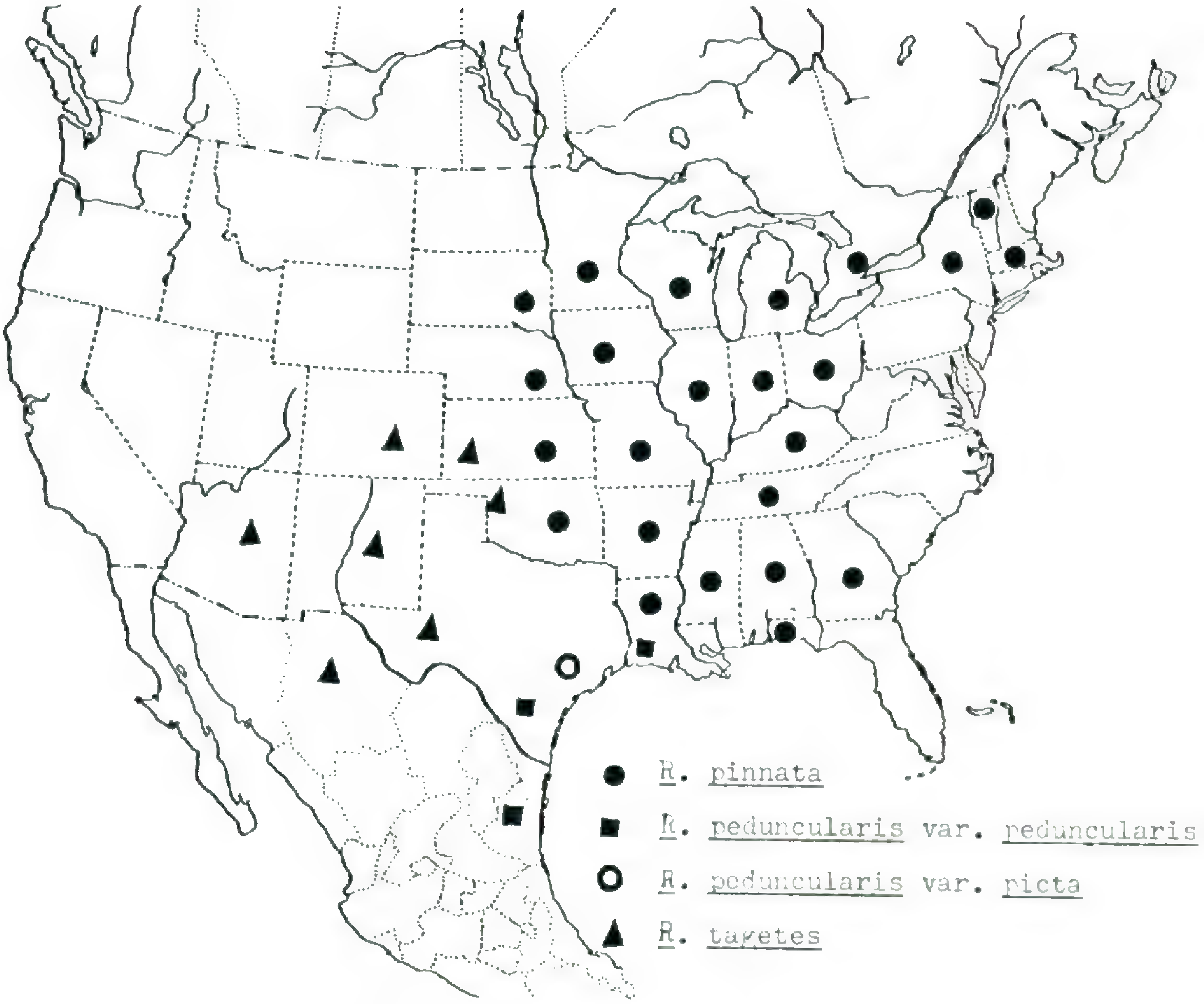

Fig. 10. Distribution of *Ratibida.*

bock Co.: *Demaree 7728* (GH, MO, US). Nolan Co.: *Tharp 47466* (TAES). Ochiltree Co.: *Cory 32228* (TEX). Oldham Co.: *Reverchon 3340* (MO). Pecos Co.: *Tharp 43939* (F, MO, NY, TEX, UC). Potter Co.: *Palmer 12534* (MO, UC). Randall Co.: *Cory 16505* (GH). Reagan Co.: *Merrill* (TAES). Reeves Co.: *Warnock 6229* (TEX). Sherman Co.: *Weaver 17800* (TAES). Sutton Co.: *Cory 15414* (LL). MEXICO: CHIHUAHUA: *Pringle 1061* (F, MO, NY).

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DEPARTMENT OF BIOLOGY
ARKANSAS STATE UNIVERSITY
STATE UNIVERSITY, ARKANSAS 72467

PLANT SPECIATION ASSOCIATED WITH GRANITE OUTCROP COMMUNITIES OF THE SOUTHEASTERN PIEDMONT[1]

W. H. MURDY

Granite outcrop communities of the southeastern Piedmont have long been of interest to the systematic botanist because of their large assemblage of endemic taxa. Crystalline rock exposures, called "flat-rocks" or "granite outcrops," occur sporadically from North Carolina to Alabama, and their combined extent is estimated to be about 12,000 acres. Ten of the best-documented species reported to be enedmic to granite outcrop communities are listed in Table 1. When their collective ranges are plotted on a single map, all ten species are found to occur within a small region of the upper Piedmont of Georgia, east of Atlanta (the innermost circle of Fig. 1). Toward the southwest and northeast the number of endemic taxa gradually decreases until only three of the species listed in Table 1 are found to be associated with granite outcrops in eastern North Carolina. This "center of endemism" in Georgia is coincident with the geographic center of the greatest concentration of exposed rock.

Table 1.

ENDEMIC SPECIES	GEOGRAPHIC ZONES (FIG. 1)					
	10	9	8	7	6	3
Isoetes melanospora	×					
Rhynchospora saxicola	×	×				
Viguiera porteri	×	×	×			
Quercus georgiana	×	×	×	×		
Amphianthus pusillus	×	×	×	×	×	
Phacelia maculata	×	×	×	×	×	
Sedum pusillum	×	×	×	×	×	
Portulaca smallii	×	×	×	×	×	×
Cyperus granitophilus	×	×	×	×	×	×
Juncus georgianus	×	×	×	×	×	×

Occurrence of 10 plant species endemic to granite outcrop communites in the Piedmont of southeastern United States.

[1]This work was supported by National Science Foundation grant NSF-GB2340.

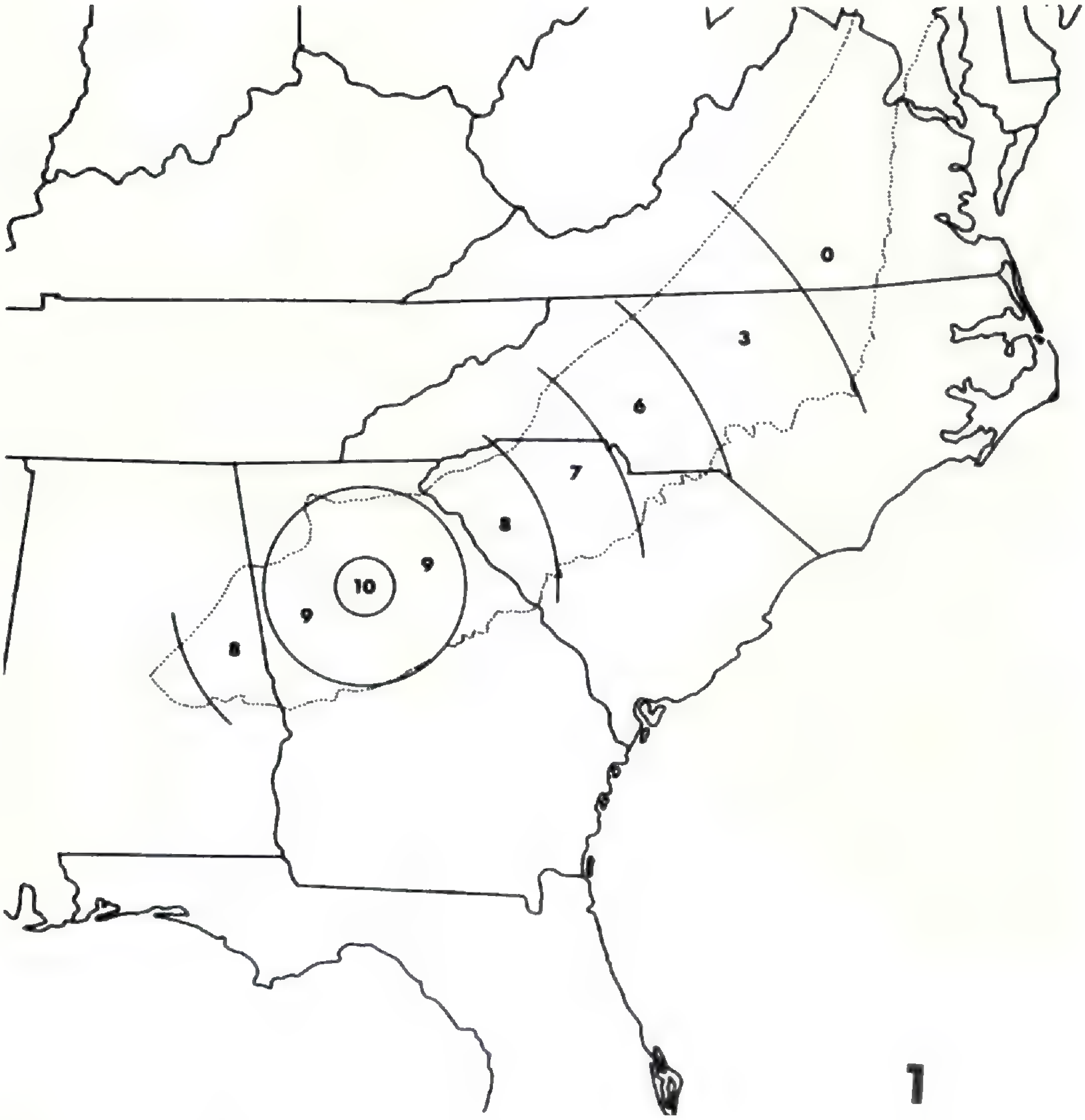

Fig. 1. Diagram to show how the number of species of granite outcrop endemics listed in Table 1 diminishes along a northeast-southwest axis from a "center of endemism" located in the central Piedmont of Georgia. The number of species is also taken as the number for the geographic zone (Table 1).

A variety of habitats are afforded by the granite outcrops. Two of the most important types available to higher plants are: 1) depression pits in the rock surface, which can be classified into a number of different community types by the correlates of soil depth and vegetation cover (Burbanck and Platt 1964); and 2) glade-like, border areas of thin soil situated between rock exposures or between rock and adjacent forest or field.

The granite outcrops have been open to plant habitation for a long period of time although the longevity of any single exposure may not be great. Sufficient time has elapsed, for example, for the rare endemic *Amphianthus pusillus* Torr. to become adapted to an exceedingly specialized and infrequent habitat. It presently occupies depression pits of a critical size, topography, soil depth, and water retentive capacity. Furthermore, it has had time to diverge from close relatives to the extent that it now constitutes a monotypic genus of uncertain taxonomic affinities. Pennell (1935), in his monograph of the Schrophulariaceae, notes that the *Amphianthus* habit of bearing flowers both on elongated floating stems and also at the base of the plant, where they are immersed and cleistogamous, has no counterpart among the Scrophulariaceae.

The strikingly high degree of endemism associated with the outcrops suggests that they have long served as active sites for speciation in the southeast. A few of the endemic species may be remnants of once more widespread species which had their origin elsewhere. However, most endemic taxa appear to have had their origin in adaptation to outcrop habitats; most by gradual, ecogeographical processes and perhaps a few by an abrupt, saltation process. The Piedmont Region marks the geographic limit of distribution for many Coastal Plain and Appalachian species and the granite outcrops provide a variety of ecologically-marginal habitats to which geographically-peripheral populations may adapt.

The processes associated with speciation may actually undergo acceleration in the region of granite outcrops. Outcrops frequently occur in clusters with exposures separated by a few miles or less, and the clusters, in turn, separated from one another by greater distances. Species characteristic of, or endemic to, outcrop communities are consequently subdivided into a number of disjunct populations. Thus, semi-isolated populations are able to diverge from nearby populations as well as occasionally cross with them. Wright (1931) considered this type of population to be capable of rapid evolution.

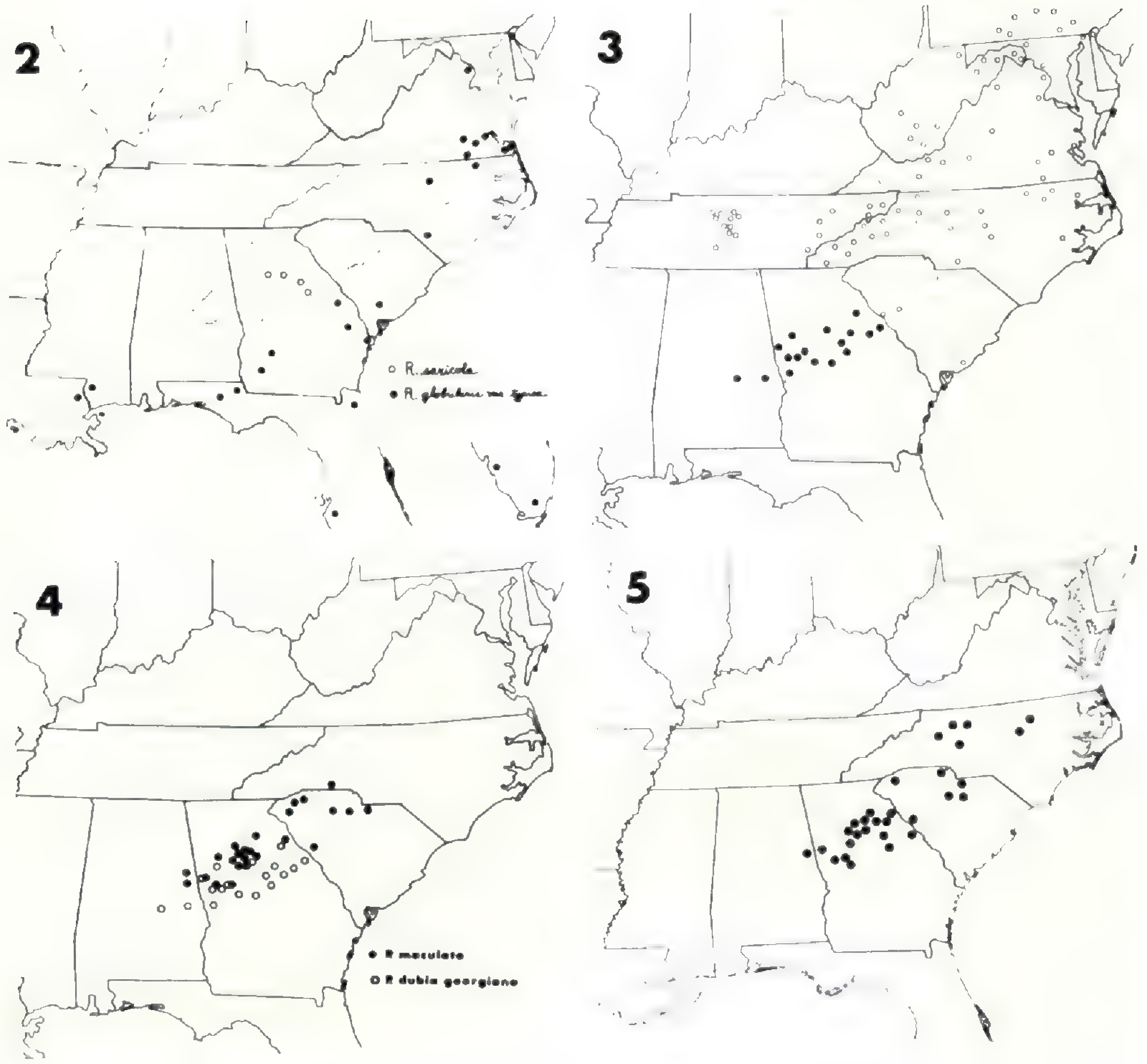

Fig. 2-5. Distribution maps. Fig. 2, *Rhynchospora saxicola* and *R. globularis* var. *typica*. Fig. 3, *Phacelia dubia* (open circles) and *P. dubia* var. *georgiana* (solid black circles). Fig. 4, *Phacelia maculata* and *P. dubia* var. *georgiana*. Fig. 5, *Cyperus granitophilus*.

ECOGEOGRAPHICAL SPECIATION

The fact that several endemic species are situated at the geographic periphery of their nearest relative is taken as indirect evidence of past ecogeographical speciation in association with granite outcrop communities. For example, *Rhynchospora saxicola* Small and *Portulaca smallii* P. Wilson occur at the boundary of the ranges of their putative, Coastal Plain progenitors, *R. globularis* var. *typica* (Gale 1944), as illustrated in Fig. 2, and *P. pilosa* (Wilson 1932, Steiner 1944, Cotter and Platt 1958) respectively. These taxa are in need of modern systematic treatment in order to more accurately assess their specific status and

evolutionary history. Another endemic species, *Phacelia maculata* Wood, which will be discussed below, is presently distributed at the southeastern boundary of the range of its closest relative, *P. dubia* of the Appalachians.

Recent ecogeographical speciation is indicated by the number of sub-specific taxa endemic to the outcrops. The systematics of one of these, *Phacelia dubia* var. *georgiana,* has been described in a recent report (Murdy, 1966). This variety was named by McVaugh (1943) as a race of *P. dubia* which could be distinguished from the latter on the basis of leaf characters. Constance (1949), in his revision of *Phacelia* species in the subgenus *Cosmanthus*, referred to it as a distinct regional phase of the Appalachian *P. dubia* restricted to granite rocks in the Piedmont of Alabama and Georgia (Fig. 3).

Population studies have revealed that the ecotype *P. dubia* var. *georgiana* can be separated from the main body of the species on the basis of any one of a number of quantitative traits, such as length of calyx, petals, and sepal hairs. The ecotype has the same chromosome number as *P. dubia* ($n = 5$) and artificial crosses between them have produced vigorous hybrids. The ecotype occurs in abundance on outcrops of the lower Piedmont (Fig. 3), and in this region, it has become an integral component of communities both in depression pits and in border areas. Its origin appears to have been recent and in the lower Piedmont. It has not yet migrated to the "center of endemism," in the upper Piedmont of Georgia, where a niche appears to be open to it.

Phacelia maculata is a species endemic to granite outcrops of the upper Piedmont from North Carolina to Alabama (Fig. 4). It is a poor competitor when compared with *P. dubia* var. *georgiana* and when both occur at the same outcrop site, the former is largely confined to deciduous glades bordering the exposed rocks, whereas *P. dubia* var. *georgiana* occupies a variety of open habitats. All of the systematic data to date suggests that *P. maculata* and *P. dubia* formerly diverged from a common, 5-chromosome

stock. Today, they are reproductively isolated by means of a postfertilization, incompatibility factor (Murdy 1966).

The tentative hypothesis is advanced that *P. dubia* is presently in the act of speciation and within recent times has produced an ecological race, *P. dubia* var. *georgiana,* at the southernmost boundary of its range and in adaptation to an ecological niche afforded by the granite outcrops. *P. maculata* may have had a similar origin in the past, but now exhibits the properties of a relict endemic because of its inability to compete successfully outside of a narrowly-restricted habitat which is gradually diminishing in extent.

SALTATIONAL SPECIATION

The occurrence of "species pairs" within outcrop communities, strikingly similar in life-form and ecology, but radically different in other important respects, suggests that saltational speciation may have been involved in their origin. The widely-fluctuating, outcrop environment would be a factor of significance in such a process. Three pairs of species will be discussed below: *Sedum pusillum* Michx. and *S. smallii* (Britt.) Ahles (*Diamorpha cymosa* (Nutt.) Britt.); *Talinum mengesii* Wolf and *T. teretifolium* Pursh; and *Cyperus granitophilus* McVaugh and *C. aristatus* Rottb. In none of these examples has a saltational mode of origin been clearly established. Instead, such a process is merely postulated on the basis of evidence presented below.

Sedum pusillum and *S. smallii*

Sedum pusillum is a small, succulent annual wholly confined to granite outcrop communities (Fig. 6, B + Fig. 8). It will grow in a variety of micro-habitats during "good" years, but is typically found growing in shallow, depression pits under the partial shade of pine or, more commonly, *Juniperus virginiana.* It is of systematic interest within the genus because of its low chromosome number, $2n = 8$ (Baldwin 1940), the lowest of any North American *Sedum.* It is of general evolutionary interest because of its endemism and remarkable similarity to *S. smallii* (Fig. 6, A). The latter is one of the most characteristic members of outcrop communities, but also occurs on sandstone outcrops

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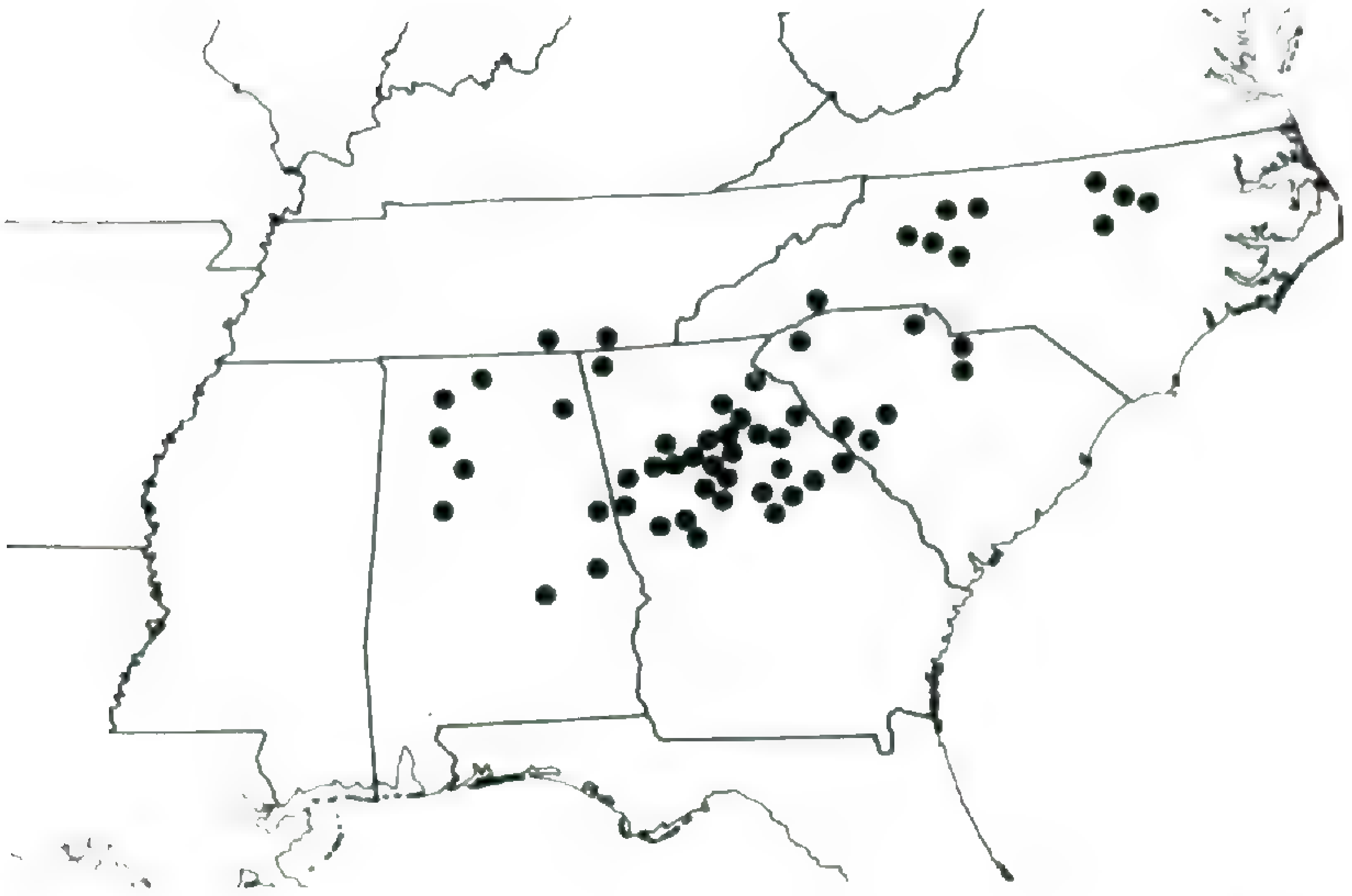

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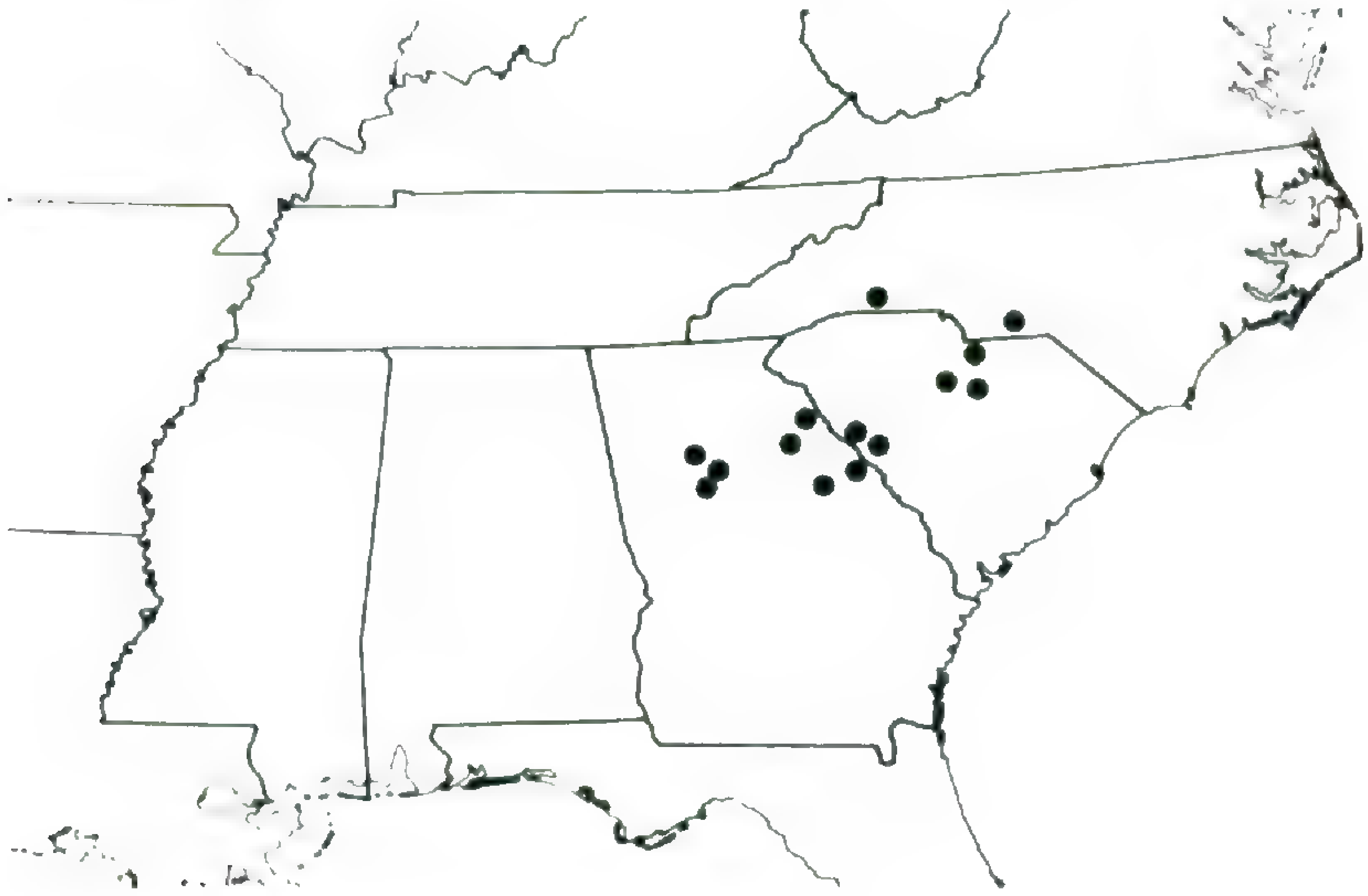

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Fig. 6-8. Fig. 6. Habit of: A, *Sedum smallii* and B, *S. pusillum*. Fig. 7, 8. Distribution maps. Fig. 7. *S. smallii*. Fig. 8. *S. pusillum*.

in Alabama, Tennessee, and Georgia (Fig. 7). It grows in abundance in the shallowest soils of depression pits where it has no competitors. Fröderström (1935), in his monograph on *Sedum,* considered the two species to be closely related. However, *S. smallii* has a very different chromosome number, $2n = 18$ (Baldwin 1940, O'Connell 1949, McCormick and Platt 1964).

Common base chromosome numbers in the Crassulaceae are 4 and 5, with most species being polyploid. The lowest numbers in each series are found in annuals (*Sedum pusillum,* $n = 4$, and *S. stellatum,* $n = 5$) within a family mostly composed of perennials. *Sedum smallii* is unusual in having a base chromosome number of 9 and Baldwin (1940) suggested that it may have originated as an amphidiploid. If this is taken as a working assumption, one of its parents could very well have been *S. pusillum,* the only extant member of the family with 4 pairs of chromosomes. Attempts should be made to produce interspecific hybrids which can be used for cytogenetic verification of the above hypothesis. For example, if 4 of the 9 chromosomes of *S. smallii* are homologous with the chromosomes of *S. pusillum,* 4 bivalents and 5 univalents should constitute the paired, meiotic condition in the hybrid. Positive results would warrant a search for the other parental species which should have 5 pairs of chromosomes.

Strong barriers to natural hybridization seem to be operative between the species. Populational analysis of a large outcrop in Rockdale County, Georgia, where both species are abundant, has yielded neither hybrids nor any indication of introgression. However, McCormick and Platt (1964) reported that: "Apparent intergeneric hybrids between *Sedum pusillum* × *Diamorpha cymosa* were observed on one outcrop out of more than 100 visited". Several hundred artificial pollinations between the two species in the spring of 1967 failed to yield any seed, while control pollinations within each species resulted in a good yield.

Talinumm engesii and *T. teretifolium*

The habit, habitat and distribution patterns of these two

Talinum species suggest that their separation into distinct, morphological entities might also have been brought about by a saltational process of speciation, which also involved polyploidy.

Talinum teretifolium ($2n = 48$) ranges from Pennsylvania to Georgia and grows in sandy or dry, rocky sites. In Georgia it is almost exclusively associated with granite exposures where it represents the only perennial in many of the shallow soils. *T. mengesii* ($2n = 24$) is found in western Georgia and it is the predominant species in Alabama, where it grows on the sandstone outcrops in Appalachian counties as well as on the granites of the Piedmont (Wolf 1939). Their ranges appear to have an allopatric pattern with a considerable overlap in Georgia. In the central Piedmont of Georgia, the predominant form is *T. teretifolium,* but pockets of *T. mengesii* populations have been located in the following Georgia counties: Douglas, Heard, Paulding, Rockdale, and Walton. Outcrops in the region of overlap support almost exclusively either one or the other species. At three sites in Georgia where plants of both species are contiguous, triploid hybrids have been found which are vigorous perennials, but apparently sterile.

The close morphological and distributional similarities between the two prompted Wolf (1939), in his evaluation of *Talinum* in Alabama, to postulate a common ancestry for them. Both species have a similar life-form and appear to occupy a very similar outcrop niche. Nevertheless, they are morphologicaly distinct species and can be readily separated on the basis of flower structure. *T. teretifolium* has small, rounded petals, fewer than 20 stamens, a short style, and flowers that open late in the afternoon, whereas *T. mengesii* has long, acute to mucronate petals, more than 40 stamens, a long, exserted style, and flowers that open early in the afternoon.

Plants of eighteen populations of *T. teretifolium,* from Georgia and South Carolina, were found to be tetraploid ($2n = 48$). Steiner (1944) gave similar counts for this

species but also reported a plant from Bibb Co., Alabama to be diploid ($2n = 24$). This is likely a case of misidentification since *T. teretifolium* has not otherwise been reported from this location which is in the heart of *T. mengesii* ($2n = 24$) territory.

It is suggested that the widespread, *Talinum teretifolium* is an amphidiploid species and that *T. mengesii* was one of its diploid progenitors. The proposed relationship for the *Talinum* species parallels that postulated for the *Sedum* species. In both pairs the polyploid member has a greater geographical range and is better adapted to exposed outcrop sites than its diploid partner, which in the case of *Sedum pusillum* is restricted to several granite outcrops in Georgia, South Carolina and North Carolina and in the case of *T. mengesii* is confined to the sandstone outcrops of Alabama and a few granite outcrops of Alabama and Georgia.

Cyperus granitophilus and *C. aristatus*

Cyperus granitophilus was first named by McVaugh in 1937 who considered it to be a form sufficiently distinct from the related *C. aristatus* (*C. inflexus*) to rank as a good species endemic to granite outcrop locations from North Carolina to Alabama. This classification was upheld by O'Neil (1942), in his taxonomic study of North and South American species of *Cyperus*, who added characters by which the two similar-looking sedges could be separated.

A recent systematic study (Wynne 1964) suggests that the endemic, *Cyperus granitophilus*, arose from the widely-distributed *C. aristatus* through autopolyploidy and subsequent selection for high ploidy levels in outcrop habitats. Data gathered from several natural populations and from herbarium specimens show the endemic to be distributed throughout the outcrop region (Fig. 5). It constitutes the predominant form in outcrop communities and grows in depression pits of little soil and scant competition. *C. aristatus*, on the other hand, is mostly found in border areas of deep soil where competition is more intense.

Plants of both species have been found to grow side by

side and both have more than once been mounted on the same herbarium sheet. Furthermore, character differences that separate them are almost all quantitative. When compared on the basis of spikelet, scale, and achene dimensions, the endemic is larger in every respect. Chromosome counts showed high, but variable, numbers within populations and *C. granitophilus* had a consistently higher chromosome number ($2n$ = ca. 80, 88, 96) than *C. aristatus* ($2n$ = ca. 48, 56, 64).

Many interesting questions have been raised by this preliminary study. One of the most widespread effects of polyploidy is to increase the water content of the cell relative to the amount of protoplasm, which in turn is believed to be a result of increase in cell size (Noggle 1949, Stebbins 1950). Could this provide increased drought resistance necessary for *C. granitophilus* to become the prevailing form in xeric, outcrop habitats? Futhermore, does this example represent a mechanism whereby a monotypic, widespread species, itself probably polyploid, could produce an ecotype able to exploit an available, but marginal, habitat by further increase in the ploidy level? Further experimental work is needed before definite answers can be given to the above questions.

CONCLUSION

The granite outcrop region constitutes an area of high endemic frequency in the southeast and the greatest number of endemic taxa occur in the central Piedmont of Georgia. Several different types of endemics are represented in outcrop communities including at least one monotypic genus, endemic species with and without related species nearby, and infraspecific taxa which appear to be ecotypes of extant species. The implication derived from this array of endemic types is that the granite outcrops have served as active sites for plant speciation for a long period of time.

The scattered distribution of rock exposures increases the probability that their populations will diverge from one another with time. An ideal situation for ecogeographical

speciation is established when such unusual and disjunct habitats are located at the boundary of a species range. Semi-isolated, geographically-peripheral populations are afforded an ecologically-marginal habitat to which they may adapt. Subsequent migration, immigration and genetical interaction among such populations could eventually produce an endemic ecotype, which, in time, could ultimately become an endemic species. This appears to be the manner by which the ecotype *Phacelia dubia* var. *georgiana* originated in the recent past from the Appalachian *P. dubia*, and may, in turn, closely parallel the manner by which the endemic *P. maculata* originated from an Appalachian progenitor in the remote past. Species which also appear to have had a gradual, ecogeographical origin, but from Coastal Plain progenitors, include *Portulaca smallii* and *Rhynchospora saxicola*.

The disjunct distribution of outcrop communities, together with their variable size and extreme environmental conditions, might all be factors contributing to the saltational origin of various taxa. Drastic fluctuations in population size could on the one hand lead to local extinction (endemic species may be totally lacking at one outcrop and abundant at another outcrop a few miles away), but could also be conducive to "catastrophic selection" (Lewis 1966), whereby a few individuals, possessing favorable genotypes, would be the sole survivors at a particular outcrop site and provide progeny for repopulation.

Three sympatric "species pairs," similar (but not identical) in vegetative morphology and in ecological adaptation, but different in other important respects, are presented as possible cases of saltational speciation. *Sedum smallii* ($2n = 18$) may have originated through allopolploidy involving the rare endemic *S. pusillum* ($2n = 8$) as one parental species and an unknown, 5-chromosome species as the other parent. *Cyperus granitophilus* may be an autopolyploid form of *C. aristatus* and appears to be better adapted to outcrop habitats than the latter. Finally, *T. teretrifolium* ($2n = 48$) may have originated as an amphidiploid with

T. mengesii ($2n = 24$) as one of its parental species. In all three examples, the polyploid member of each pair is more widely distributed than its diploid, or, in the case of *Cyperus*, its lower polyploid relative.

DEPARTMENT OF BIOLOGY
EMORY UNIVERSITY
ATLANTA, GEORGIA 30322

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A NEW SPECIES OF PHYSALIS FROM THE GALAPAGOS ISLANDS

U. T. Waterfall

While preparing a treatment of *Physalis* for A Flora of the Galapagos Islands by Ira L. Wiggins of Stanford University, it became evident that some of the material under consideration was not readily referable to a known species. The following species is therefore described.

Physalis galapagoënsis Waterfall, sp. nov. Planta herbacea, annua, 15-90 cm alta; ramis, petiolis et pedicellis plus minusve antrorse hispidulis; foliis ovatis, marginibus inaequaliter crasse dentatis, principalibus 3.5-8 cm longis et 3-6 cm latis, petiolis 1.5-5 cm longis; calycibus floriferis 2.5-5 mm longis et 1.5-2 mm latis ad basim loborum; calycis lobis lanceolatis vel anguste lanceolato-attenuatis, (1-) 2-3 mm longis; pedicellis floriferis 4-6 mm longis; corollis luteolis, immaculatis, 4-6 mm longis; antheris luteis vel marginibus violaceis, oblongis vel ovato-oblongis, 1-1.5 mm longis; filamentis 1.5-3 mm longis; calycibus fructiferis pentangulatis, glabris, 30-45 mm longis et 37-40 mm latis; calycis lobis lanceolatis vel anguste lanceolato-attenuatis, 4-8 mm longis, interdum abrupte porrectis; pedicellis fructiferis 15-30 mm longis; baccis 12-15 mm latis.

TYPE: *Ira L. Wiggins 18724*, Feb. 15, 1964, on nearly bare lava ridge at dormitories, vicinity of Charles Darwin Research Station, Acadamy Bay, Isla Santa Cruz, Galápagos Islands, Ecuador (DS; Isotype: OKLA).

OTHER COLLECTIONS SEEN: ALBEMARLE ISLAND: Villamil, Apr. 27, 1932, *John Thomas Howell 8939* (CAS); abundant near beach in shady places, Tagus Cove, *R. E. Snodgrass & E. Heller 185*, Mar. 1899 (DS); in shady places around 900 ft., Tagus Cove, *Alban Stewart 3393*, Mar. 24, 1905-1906 (CAS); CHARLES ISLAND: Post Office Bay, *John Thomas Howell 8814*, Apr. 23, 1932 (CAS); in shady places near shore, *Alban Stewart 3397*, May 24, 1905-1906; CHATHAM ISLAND: corolla yellow, concolorous, Wreck Bay, *John Thomas Howell 8524*, Apr. 15, 1932 (CAS); GARDEN ISLAND: near Hood Island, *John Thomas Howell 8772*, Apr. 22, 1932 (CAS); HOOD ISLAND:*R. E. Snodgrass & E. Heller 740*, May 1899 (DS); INDEFATIGABLE ISLAND: corolla greenish-yellow, Acad-

emy Bay, *John Thomas Howell 9020*, May 2, 1932; JARVIS ISLAND: *John Thomas Howell 9759B*, June 6, 1932 (CAS); NORTH SEYMOUR ISLAND: *John Thomas Howell 9962B*, June 11, 1932 (CAS); SANTA CRUZ ISLAND: near Charles Darwin Research Station in *Bursera* forest, alt. 30 meters, *Syuzo Itow 267*, Feb. 23, 1964, (DS); vicinity of Charles Darwin Research Station, Academy Bay, in partial shade among Opuntia echios trees, sea level to 30 meters, *Ira Wiggins 18314*, Jan. 23, 1964 (DS).

Physalis galapagoënsis is characterized by its small, immaculate corollas, small anthers, yellow all over or violet-margined, and its usually large, glabrous, 5-angled fruiting calyces, much-inflated about the berry.

In the latter characteristic it is reminiscent of *P. cordata* Miller, a common species of southern Mexico, Central America and the West Indies (Waterfall, 1967), a species with much larger, dark-maculate corollas. Or it might be compared with the less common *P. porrecta* Waterfall (l. c. 237, 238) of Oaxaca, Costa Rica and Guatemala, a species with abruptly-beaked fruiting calyces and large corollas, immaculate, or inconspicuously spotted. The length of the corollas is similar to that of *P. clarionensis* Waterfall (l. c. 326, 327) from Clarion Island off the coast of Baja California, but the latter species has shorter, and proportionally narrower, fruiting calyces.

The chromosome count, according to the label is: $n=12$ (by Kyhos) based on 10 cells.

DEPARTMENT OF BOTANY AND RESEARCH FOUNDATION
OKLAHOMA STATE UNIVERSITY
STILLWATER 74074

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A FREEZE-DRY TECHNIQUE FOR THE PLANT COLLECTOR

RICHARD A. HOWARD

During a visit to the United States several years ago Dr. Hans-Christian Friedrich, Oberkonservator at the Munich Botanic Garden, described his work with the extremely succulent plants of Southwest Africa. In replying to a question on the preparation of herbarium specimens from such materials he reported on the success they had had in freezing the plants from a greenhouse collection in Munich and then drying the plant specimens in a plant press in the fashion familiar to collectors. The implication was made that the liquid from the plant tissues nearly "flowed out" of the defrosted specimens in the drying process. It was my feeling at that time that the technique might be useful also in meeting two distinct problems I had encountered in collecting plants in the American tropics. The first concerned the preparation of some of the fleshy or latex-possessing tropical plants encountered in field work in the Caribbean Islands. Specimens of the Cactaceae, Euphorbiaceae, Polygonaceae and Vitaceae usually dry slowly, fragment at nodes or articulations, discolor, become distorted in shape, or adhere to the drying papers. Suggestions have been made previously to overcome these problems involving treatment of specimens with solutions of formaldehyde, alcohol or chemical fixatives, or boiling in water. All of these techniques have been used at times with varying degrees of difficulty in the field and of success in the preparation of dried specimens.

The second problem occurs in the course of field work when the amount of rare or unusually high quality material to be pressed and dried exceeds the capacity of the drying apparatus. In tropical areas this material cannot be stored fresh in plastic bags or held loosely in buckets of water or even lightly contained in improvised presses without some deterioration of the specimens. In their Manual for Tropical Herbaria (Regnum Vegetabile 39: 45-48. 1965) Fosberg and Sachet summarize the various techniques that have been

developed in the tropics of both hemispheres for collecting plants in quantity and sending the material back to a distant base for arrangement later into individual specimens and for drying. These techniques call for arranging the specimens in papers alone or in presses and placing such bundles in plastic sheets, tubes or containers, or in metal cans to be sealed after alcohol, formaldehyde or other chemicals have been used to soak, paint, dust or immerse the specimens.

Both of these problems were encountered again during the summer of 1967 in the course of field work in St. Kitts and in Puerto Rico. Mr. Robert Wadsworth, who was collecting representative specimens on the former island as part of a study of the dwarfed elfin vegetation in the Antilles, worked with very limited drying facilities. At one stage of the operation a chest-type household freezer was made available through the courtesy of Mr. Colin Napier of St. Kitts. The plant specimens were prepared in the usual manner and the portion of the day's work which could not be accommodated on the small heater frame were placed in the freezer. Eventually, when space became available, the frozen press was removed from the freezer and placed directly on the heater. Now that all the specimens are mounted for insertion in the herbarium the frozen, then dried, specimens are indistinguishable in most cases from those dried directly from the field.

In Puerto Rico we had the opportunity of using the same technique while also making some comparative tests of the freezer-heater combination. Plants known to be difficult to prepare as specimens were deliberately chosen for trial. Mr. Joseph B. Martinson, who has supported many peculiar requests in relation to our study of the vegetation on Pico del Oeste, tolerated the use of his chest type of freezer. The cooperation of Dr. and Mrs. Richard J. Wagner and of Mr. Luis Maldonado helped complete the studies.

Our attempts to hold general collections for several days by freezing them and then completing the drying process were successful. There was some indication that the drying

process was slower than with freshly pressed specimens, but for the majority of collections the specimens prepared by the two methods were indistinguishable.

Specimens of certain native plants from the Luquillo Mountains and of certain species under cultivation by Mr. Martinson and at the Pennock Nurseries in Hato Rey were prepared in equal sets for comparative processing studies. One complete set was placed in a press and dried immediately, using electric space heaters with low-speed blowers. Other sets were prepared in presses and frozen for 48 hours. One of these was allowed to defrost to air temperature before it was placed on the heater, while a comparable set was placed on the heater directly from the freezer.

The fresh material which was placed directly over the heat without freezing dried from the lower side of the press, as expected, unless the specimens were rotated. The loss of liquid from the specimens was gradual and the separators rarely became very wet. The frozen material, however, tended to lose liquid quickly when defrosted so that the papers, blotters, or separators became saturated. Unless these were changed frequently the specimens often developed a growth of mold and the presses ultimately required 10-25% more time on the heater than did the fresh material. Recent correspondence with Dr. Friedrich reveals that he, too, experienced the problems of rot and fungus attack, which he controlled by soaking the press with alcohol after the first 24 hours of drying.

Only after several unsatisfactory attempts to use the freezer as an aid to plant collecting did we finally develop the technique and knowledge necessary to recommend it to those collectors fortunate enough to have a freezing compartment handy. For leathery or succulent specimens or those with thickened portions such as the large inflorescences of the Araceae or Musaceae, the stems or rhizomes of the Zingiberaceae, the rosette bases of the Bromeliaceae, or the pseudobulbs of the Orchidaceae, the freezing technique has real advantages. The specimens can be prepared whole or cut longitudinally and frozen either in newspaper

in the freezing compartment of a refrigerator, with dry ice in a chest or box, or in a loose press in a larger freezing unit. The frozen material is then returned to air temperature with the press loosely arranged. The liquid will often drain out of the specimens by gravity and the wet papers of the press must be changed. They now can be placed in a press and the pressure increased slightly or gradually for several hours to squeeze out more liquid before the specimens are finally placed on dry papers and arranged in a press for drying over heat. These specimens will dry more rapidly than fresh material since the liquid has been released from all of the tissues simultaneously. With this preliminary treatment the actual drying time is reduced 25 to 50%.

The benefits of this method of handling certain kinds of plant materials are evident on a comparative basis. There is a noticeable reduction in the fragmentation of stems at nodes, the disjunction of leaves from stems, the separation of parts of compound leaves, and the fragmentation of inflorescences. The parts of inflorescences of plants of *Heliconia* and *Musa* or various members of the Araceae or Zingiberaceae remain distinct, and single flowers or fruits can be lifted free when dry. This result contrasts dramatically with the agglutinated mass that is usually formed when the specimens are dried directly over heat. There is also less tendency for the specimens to adhere to the pressing papers. Succulent stems or woody ones which contain large amounts of liquid also dry more quickly after being frozen and tend to retain a more natural shape and color. There is much less distortion of fleshy parts of the plants if the pressure of the press is not excessive. Tracings were made of leaves of *Alloplectus* and of *Begonia* before and after drying and freeze-drying. Although both species showed the translucent characteristic of frozen material, the final leaf shape was less distorted and more truly representative of the fresh condition than was the material dried directly. The translucent condition of frozen-dried material even has an advantage in revealing more easily the vascular patterns.

In general, there was also a lessening of the darkening in those species which tend to darken on drying if the specimens had been frozen. There were, however, some notable exceptions.

The following materials have been treated by freeze-dry technique. Specimens cited bear the collecting numbers of the author and a representative set is deposited in the herbarium of the Arnold Arboretum, Harvard University.

Alocasia sp. Araceae *(17041)*. A stout herb under cultivation with very thick inflorescence and rhizome. The stems, inflorescence, and petiole sections retained a more characteristic shape after freezing.

Alloplectus ambiguus Urb. Gesneriaceae *(16641, 16815)*. An epiphytic herb with succulent stems and foliage. The frozen specimens have a translucent appearance, while heat-dried specimens tend to darken. The fleshy fruit is much less distorted after freezing.

Anthurium dominicense Schott. Araceae *(16642)*. An epiphytic rosette-forming plant with succulent and leathery leaves. Heat-dried specimens turn a pale brown color, while freezing causes a blackening of the leaves. The rhizomes retained more natural shape after freezing. All specimens proved to be very susceptible to fungus attack during drying.

Begonia decandra Par. Begoniaceae *(16939)*. A terrestrial herb with normally pink-colored translucent succulent stems and leaves. Heat-dried specimens tended to darken, while those frozen before heat drying became more translucent and dried a lighter color. Fragmentation of the leaves from the stems or of the inflorescense was conspicuously less in the material which had been frozen.

Caryota sp. Palmae *(16912)*. A cultivated stout cane-type fishtail palm. Both inflorescences and leaves were prepared. The frozen leaves retained a green color while the fresh material darkened. The flowers and young fruits are retained on the rachi much more securely in the frozen material. The mature flowers, however, fell from the rachus in both methods of preparation.

Cissus trifoliata L. Vitaceae. An herbaceous vine which has succulent leaves and stems. The fresh dried specimens showed the fragmentation botanists have come to expect with most tropical species of *Cissus*. A considerable reduction in fragmentation was evident in the specimens which had been frozen. The leaflets were retained intact in most cases and the stem fragmented only at the very young nodes.

Clusia grisebachiana (Pl. & Tr.) Alain. Guttiferae *(16632)*. Small tree with thick coriaceous leaves and copious latex in tissues of leaf and stem cortex. Fruits thick and inflorescence commonly fragile. Specimens dried noticeably faster after freezing and retained a clearer yellow-tan color. The fragility was not reduced in any noticeable manner.

Epidendrum ramosum Jacq. Orchidaceae *(16640)*. Epiphytic. This species of orchids tends to break apart in normal drying. The frozen specimens retained their leaves in more satisfactory numbers, but the specimens were abnormally translucent when dried.

Forsteronia portoricensis Woodson. Asclepiadaceae *(16637)*. This is a rampant vine with heavy semi-fleshy leaves, abundant latex and deep carmine red flowers. The fresh-dried specimens showed the dark brown or black discoloration often obtained with plants having a latex. The specimens which had been frozen first became an unexpected greenish-brown color.

Guzmannia berteroniana (R. & S.) Mez Bromeliaceae *(16638)*. An epiphytic rosette plant with conspicuously bracted inflorescence. Following the usual practice the rosette was reduced to one quarter the original size before processing. In some specimens the inflorescence was split down the middle before drying. This plant does not produce beautiful herbarium specimens with any technique. The fresh-dried material showed the straw-brown color characteristic of most herbarium specimens. The frozen material retained a greenish cast. The colorful bracts and flowers discolored in both processes but the parts were more easily separated in the frozen specimens.

Hedyosmum arborescens Sw. Chloranthaceae *(16633)*. A tree with fragile branches, abundant liquid in the stems, succulent leaves, and white fleshy perianth parts to the fruit. All Caribbean material of *Hedyosmum* shrinks noticeably in drying and turns a characteristic chocolate brown. In this test the frozen material showed a slight translucence not noticeable in heater-dried material.

Heliconia bihai L. Musaceae *(16643)*. A clump-forming herb with succulent petioles and a thick distichous inflorescence. Material was prepared of the leaf blade and the petiole base, and of the inflorescence, which was split longitudinally. *Heliconia* specimens are notoriously difficult to dry. Several collectors have attempted to boil the specimens before drying, with very unsatisfactory specimens resulting. In this test all frozen material dried much more rapidly and made much better looking specimens. The frozen leaves retained a better color. The frozen inflorescense was flatter, but the individual flowers could be separated easily and the fruits remained distinct, very much in contrast to the heater-dried material.

Hillia parasitica Jacq. Rubiaceae *(16634)*. An epiphytic or climbing succulent woody plant with pendant branches. The long white tubular flowers are fleshy and the leaves are thick. The specimens dried by heat alone showed the characteristic black color of most herbarium specimens, while the flowers are an ivory white color. Following freezing, however, the leafy specimens were less discolored and a lighter green color suggesting a translucence, while all of the flowers were either pale tan or brown with a definite translucent aspect.

Musa sapientum L. Musaceae *(16938)*. A succulent herb with massive inflorescence. Herbarium specimens of banana inflorescences are infrequent in herbaria. Very young inflorescences were split lengthwise for this test, while older ones were separated into bract and flower components for both pistillate and staminate flowers. The heater-dried material discolored and became distorted in shape. The frozen material dried more quickly, showed similar discoloration but much less distortion.

Philodendron aff. *bipinnatifidum* Araceae *(16928)*. A heading type of *Philodendron*. Inflorescences were split and frozen, then defrosted and placed in press for drying. Regular drying methods produced much-distorted specimens in which the flowers and fruits were tightly agglutinated. Freezing produced equally darkened specimens, slightly less distorted but with separate flowers and young fruits. Leaves dried and darkened in both techniques.

Philodendron krebsii Schott. Araceae *(16644)*. A high-climbing herbaceous vine with succulent stems and leaves and a fleshy inflorescence. Normal heater drying produced the usual blackened specimens and agglutinated inflorescences. Material which had been frozen before drying was tan or light brown in color and the spathe and spadix separated more readily for dissection.

Pitcairnia angustifolia L. Bromeliaceae *(16636)*. A rosette-forming terrestrial plant with stout inflorescence axil and red succulent fruits. Heater-dried material turned a straw-brown color, while the frozen and dried material retained the natural glaucous-gray color. In flower and fruit, however, the plant parts showed better natural pigmentation when dried directly.

Plumeria alba L. Apocynaceae. The stout stems of *Plumeria* contain copious amounts of a low viscosity latex which causes specimens dried normally to adhere to paper. The flowers are fleshy and in normal drying techniques discolor slightly and usually fall free from the inflorescence. The Puerto Rican specimens tend to have the leaves more tightly curled or involute than those of other West Indian populations. The frozen dried material produced noticeably flatter leaves with a slight degree of translucence. The frozen flowers were conspicuously translucent but were not held on the inflorescence to any greater degree. Frozen material generally did not adhere to the drying papers.

Vriesia sintenisii (Baker) Sm. & Pittend. Bromeliaceae *(16639)*. An epiphytic plant with a rosette of leaves and a stout erect rhizome. This species under normal preparation does not make attractive specimens. Those dried from

fresh condition showed considerable shriveling of the leaves, contraction of the inflorescence, and general darkening of the specimen. The frozen material, in contrast, retained a more natural form of rosette and leaves, and all parts showed more natural pigmentation.

Not every expedition to a tropical area will be fortunate enough to have a freezer with space available at a base camp. When such circumstances do occur or when it is necessary to prepare unusually succulent materials in other surroundings, the freezer may aid the collector in holding massed collections and in speeding the drying while improving the technique for processing difficult materials.

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ARNOLD ARBORETUM
JAMAICA PLAIN, MASSACHUSETTS

NOTES ON ROCKY MOUNTAIN CARICES

F. J. Hermann

In the preparation of a *Manual of the Carices of the Rocky Mountains and Colorado Basin* (to be published in the Agriculture Handbook series of the U. S. Department of Agriculture) the need for a change in status for several taxa and for proposing two new varieties became apparent. These are as follows:

Carex foenea Willd. var. **tuberculata** F. J. Herm., var. nov. A varietate typica recedit perigyniis ventraliter tuberculatis.

This variety differs strikingly from the typical form of the species in having the perigynia ventrally granular-tuberculate, much as in *C. potosina* Hemsl. of Mexico. It is a variable characteristic in the present taxon, being sometimes very prominent but in other collections barely perceptible. Since it appears to be geographically segregated, apparently never occurring in eastern United States where the species is not uncommon from Maine to New Jersey, varietal status seems most appropriate for it.

SPECIMENS EXAMINED: WASHINGTON: Mission Peak headwaters, alt. 6000 ft., Wenatchee National Forest, Chelan County, *G. Garrison, D. Wooldridge & R. Gibbons* 80-56, July 24, 1956 (TYPE — US; isotype — USFS); COLORADO: Rio Grande National Forest, alt. 10,800 ft., *D. C. La Font 18,* (USFS); north shore of Trappers' Lake, Garfield County, alt. 9500 ft., *F. J. Hermann 5433,* (US); NEW MEXICO: West Fork of Tusas River, Carson National Forest, alt. 9500 ft., *R. F. Copple 240,* (USFS); ALBERTA: in sand under Jack pines, 15 mi. N. of Fort Saskatchewan, *G. H. Turner,* July 2, 1937 (US).

Carex vallicola var. **rusbyi** (Mack.) F. J. Herm., comb. nov. *C. rusbyi* Mack., Smithson. Misc. Coll. 657: 2. 1915.

Intermediates between this plant of the mountains of Arizona and New Mexico and the more wide-ranging *C. vallicola* are too frequent to warrant its retention in specific rank.

Carex microptera Mack., var. **crassinervia** F. J. Herm., var. nov.

A forma typica differt perigyniis ventraliter valde 5-7-nerviis.

In typical *C. microptera* the perigynia are lightly few-nerved ventrally, the nerves often being evident only at the base. The present plant is in striking contrast to this with its very stout 5-7 ventral nerves.

SPECIMENS EXAMINED: COLORADO: open parks, basin below Engineer Pass, alt. 11,000 ft., Ouray County, Colorado, *W. M. Johnson 594*, Aug. 14, 1967 (TYPE — US); Wyoming: moist meadow (Beartrap Meadows) at edge of forest, west of Circle Drive road, summit of Casper Mountain, alt. 7900 ft., Natrona County, *F. X. Jozwik 262* (USFS).

Carex luzulina Olney var. **ablata** (Bailey) F. J. Herm., comb. nov.

C. ablata Bailey, Bot. Gaz. **13**: 82. 1888, not Boott *apud* Miq. 1867.

The great frequency of transitional forms between this and typical *C. luzulina* make it impractical to attempt to maintain it in specific rank as was done by Mackenzie.

Carex parryana Dewey, var. **brevisquama** F. J. Herm., var. nov.

"*C. aboriginum* M. E. Jones", Mack., N. Am. Fl. **18**: 364. 1935, not M. E. Jones, 1910.

A varietate typica recedit spica terminali staminata, spicis femineis 4-5 mm. latis, squamis femineis perigyniis conspicue brevioribus, perigyniis 2.75-3.5 mm. longis, 1.75-2.5 mm. latis.

Dr. Arthur Cronquist, in his studies of the flora of the Great Basin, first noted the discrepancy between Mackenzie's "*Carex aboriginum*" and Jones' type of that species, which is still the only collection known, and called it to the attention of the writer. Mackenzie's concept may be separated from typical *C. parryana* by the following key:

Terminal spike usually gynaecandrous; pistillate spikes 2-3 mm. wide; pistillate scales mostly equaling to exceeding and concealing the perigynia; perigynia 1-1.5 mm. wide, 2-2.5 mm. long .... *C. parryana*

Terminal spike staminate; pistillate spikes 4-5 mm. wide; pistillate scales 1/2-2/3 the length of the perigynia; perigynia 1.75-2.5 mm. wide, 2.75-3.5 mm. long .... *C. parryana* var. *brevisquama*

Carex heteroneura W. Boott var. **epapillosa** (Mack.) F. J. Herm., comb. nov.
C. epapillosa Mack. in Rydb., Fl. Rocky Mts. 138. 1917.

This and the following two sedges are amply distinct from *C. heteroneura* in their extreme forms, but intergrading forms between all four taxa occur with such frequency that attempts to maintain them in specific rank have been impractical.

Carex heteroneura var. **chalciolepis** (Holm) F. J. Herm., comb. nov.
C. chalciolepis Holm, Am. Jour. Sci. **IV. 16**: 28. 1903.

Carex heteroneura var. **brevisquama** F. J. Herm., var. nov.
C. atrata auct. Amer. (including Mackenzie, N. Am. Fl. 18: 371. 1935), not L., Sp. Pl. 976. 1753.

True *Carex atrata* L. is Eurasian and is not known to occur in America. It belongs to the group in Section Atratae having subinflated, scarcely flattened perigynia. The American plant that has been passing as *C. atrata*, although it often merges more or less into *C. heteroneura* and the above two varieties, is sufficiently different from all of these in its typical form to merit varietal recognition.

FOREST SERVICE HERBARIUM
RANGE AND WILDLIFE HABITAT RESEARCH
U. S. DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

BOOK REVIEW

The Evolution and Classification of Flowering Plants by Arthur Cronquist, Senior Curator, The New York Botanical Garden. Houghton Mifflin Company, Boston. 1968. i-xii, 1-396, with glossary. $6.95.

As the title implies, this book is conveniently divided into two sections. The first, which amounts to approximately one-third of the work, is concerned with taxonomic principles, the origin of the angiosperms, and the evolution of characters. The second and by far the longer section is devoted to the author's classification of the angiosperms (Magnoliophyta) and to explaining in some detail his reasoning in erecting the proposed system.

The first chapter deals with certain taxonomic concepts such as the natural system, character values, monophylesis, parallelism, survival value (adaptive significance) of certain characters, and the grouping and ranking of taxa. This chapter, as the other two in the first section, ends with a short list of selected references. In general, the discussion is interesting, although the topics are highly selective.

One might disagree that the best definition of taxonomy is "a study aimed at producing a system of classification of organisms which best reflects the totality of their similarities and differences", even though the author readily admits that "taxonomy might be variously defined, according to the definer . . .".

A biochemist might also disagree with the statement that we know perhaps more about man than about any other species in light of the recent statement of one molecular biologist that we now know at least one-fifth and maybe more than one-third of all the chemical reactions in *Escherichia coli.*

On the other hand a palynologist might take the author to task for the statement on page six that identifications of fossil pollen "cannot provide new or independent information on the evolutionary diversification of a group, or on the transitions between groups; they merely document the existence of a modern group at a particular time in the past".

Among the major conclusions of this chapter are the following: taxonomy is based on multiple correlations, character value is determined *a posteriori,* the presence of a character is likely to be more important than its absence, and a proper taxonomic system must reflect evolutionary relationships.

The second chapter very briefly characterizes the angiosperms, reviews the fossil record (or lack of it), and surveys the groups that have been suggested as possible angiosperm precursors: conifers, the Gnetales, and various cycadophytes — cycads, the Bennettitales, the Caytoniales, and the seed ferns. After eliminating most of the above groups as potential ancestors, the author concludes, as so many others have in the past, that although there is a vast abyss between the seed ferns and the angiosperms, the former are the best candidate for the ancestors of the angiosperms.

The third and final chapter of the first section deals with the evolution of characters. The topics covered are the determination of primitive characters and evolutionary trends, the characters of the primitive angiosperms, and finally a relatively lengthy discussion of the evolutionary morphology of the angiosperms beginning with habitat and growth habit, proceeding through leaf structure, vascular structure, inflorescences, and flower structure, and ending with fruits and seed dispersal.

The chapter ends with another discussion of the non-adaptive value of the majority of the characters of the higher angiospermous categories. A previous dicussion of the same topic is to be found under the heading "Ecologic Niches, Survival Value, and Taxonomic Groups" in the first chapter. The author is well known for his somewhat unorthodox views concerning this subject and for various papers on orthogenesis in the angiosperms. He himself admits that this viewpoint is "not in favor among most modern students of evolutionary mechanisms, who feel that any evolutionary trend must ultimately be related to survival value". Perhaps this is the reason that the term

"orthogenesis is not to be found even once in the book, such phrases as "evolutionary momentum" or "predisposed evolution" being used in its place.

Evidently the author has not recognized the possibility that while the higher angiosperm categories *per se* may not have evolved in response to a certain adaptive zone (*fide* Simpson), the majority of the individual characters of the higher categories may themselves be adaptational and have their origin in natural selection.

Be that as it may, the discussion in the first part of the book (and indeed in the whole work) airs a number of good ideas which are expressed in a refreshing style. The following excerpts are taken as examples:

> Evolutionary trends have all degrees of stability, from those which are so vague and subject to reversal that they can scarcely be recognized as trends, to those which fasten an inescapable grip on the destiny of the group. p. 62.

> My nose tells me that the ethereal oils in the Magnoliidae are all chemically allied, and different from the ethereal oils found in other groups of flowering plants, but I have not found an account of the chemistry. p. 135.

> To borrow an analogy which Stebbins has used in another context, evolutionary increase in parts of relatively small and definite number follows a goatpath, whereas reduction follows a paved highway. p. 313.

> Anyone who has pushed a lawnmower should recognize the significance of the intercalary meristem in permitting a plant to withstand grazing. p. 344.

The last two-thirds of the book is a rather lengthy exposition of the author's system of angiosperms. Each recognized order is discussed, followed by a very useful synoptical key to the families of the order. This is followed by selected references of predominantly recent vintage.

Six subclasses of dicots and four monocots are recognized. The dicot subclasses and roughly their composition are as follows:

1) the Magnoliidae, which is a slightly restricted concept of the Englerian order Ranales.
2) the Hamamelidae, which is basically the Amentiferae.
3) the Caryophyllidae or Centrospermae.
4) the Dilleniidae, which is primarily the Englerian order Parietales with the ericaceous and ebenaceous Sympetalae thrown in along with a few other groups such as the Malvales, the Lecythidaceae, and the Capparales.
5) the Rosidae, which includes among others the sapindalean-geranialean complex, the Myrtales, the Euphorbiales, and the Umbellales.
6) the Asteridae, which includes the epigynous Sympetalae (Rubiaceae, Compositae, etc.) and the remainder of the hypogynous Sympetalae other than the Ericales and Ebenales (i.e., the Contortae and the Tubiflorae).

A few comments on certain specific points of the system will now be made.

It is evident that the author has made use of a number of personal communications and pre-publication manuscripts. It is unfortunate, however, that he was not able to discuss the Hamamelidaceae with Dr. A. L. Bogle, who for the past several years has been investigating the floral morphology and vascular anatomy of the family. Unpublished evidence available from this research strongly suggests that several genera of the family (e.g., *Distylium, Sycopsis*) possess bisexual pseudanthia (thus contradicting the key to the subclasses of Magnoliatae, p. 131), that the petals of the Hamamelidaceae are staminal in origin rather than of the probably more primitive tepalar origin (resulting from the differentiation of a primitively undifferentiated perianth of tepals into a petaloid upper part and a sepaloid lower part — as in the Magnoliaceae), that the flowers of the family were primitively apetalous, and that the supposedly primitive position of the genus *Disanthus* is at best questionable.

In light of this knowledge one might justifiably disagree with the author's statement that the Trochodendrales "have already progressed farther in floral reduction than the Hamamelidaceae, which have unmistakable (though somewhat reduced) petals, in contrast to the complete absence

of petals in the Trochodendrales". Conceivably the sepaloid perianth in *Tetracentron* may represent the vestiges of a once undifferentiated perianth while both the Trochodendrales and the *more primitive* members of the Hamamelidaceae are apetalous. Thus the problem of how to account for the petals in some members of the otherwise more advanced Hamamelidaceae vanishes when one considers that these petals may have arisen secondarily from apetalous ancestors by sterilization of stamens and do not represent petaloid vestiges of a once undifferentiated perianth.

The author's concept of the Rafflesiales as having "rather large to very large flowers" leads him to conclude among other things that a notable difference between that order and the Santalales is the size of the flowers. However, genera with very small flowers such as *Apodanthes* and *Pilostyles* immediately come to mind, even though the largest flower known is in the genus *Rafflesia*. Also this group is not composed solely of root parasites as the author implies, since certain members occur on the stem and minor branches of their host.

The author's treatment of the monocots is somewhat novel, but I am not in a position to comment on the Commelinidae and the Liliidae. The placement of the Juncales warrants some attention and is an interesting treatment of the group.

Unfortunately, the book is too short to treat familial relationships in any detail. It is to be regretted that a further treatment at the family level as is done in the latest book by the Russian phylogenist Takhtajan was not possible.

A chart showing the over-all classification at the ordinal level would be greatly desirable. Attention should also be called to the fact that families which the author does not accept are often not mentioned in the body of the discussion and their placement in the system can only be determined by reference to the list of families and orders at the end of the book.

The great number of personal communications and pre-publication manuscripts alluded to will certainly help to keep the book up-to-date longer than usual. There is a good coverage of new chemical data as they relate to phylogeny and the reader is especially referred to the excellent discussion of betalains in the Caryophyllidae (Centrospermae).

One of the major accomplishments of both Cronquist and Takhtajan is the erection of six rather large and for the most part probably natural subclasses within the dicots. The erection of these major divisions greatly aids one in grasping the prominent evolutionary trends within the dicotyledons. At last the major patterns are emerging and the work of the future phylogenist will consist mainly of deciding where to place a certain family or order here and there, i.e., it will be a matter of filling in the details and confirming previous ideas.

Although obviously opinionative, the author's frankness on certain morphological questions is quite refreshing. This includes his ideas on such topics as the following:

1) that the staminal fascicles in many of the Dilleniidae *sensu* Cronquist represent fusion and reduction rather than splitting and multiplication.
2) that the tendency in the Apocynaceae-Asclepiadaceae for a separation of the pistils from the base upwards is secondary rather than primary.
3) that the centrifugal maturation of the stamens in the Winteraceae (or in any family for that matter) is not phylogenetically significant; rather it is the centrifugal versus centripetal direction of the *initiation* of the staminal primordia which has phylogenetic significance.

In conclusion, the book should be read by every botanist who is interested in the latest thoughts concerning the phylogenetic treatment of the flowering plants. It is the most detailed treatment of a modern "Besseyan-based" system of angiosperm classification in English, being second only to the more detailed work of Takhtajan (unfortunately in Russian). The book should also serve admirably for plant taxonomy courses as a supplement to the usual

morphology and taxonomy texts. It will serve to put the orders and families of angiosperms into better perspective in the light of modern phylogenetic thought, which is something that is often sorely neglected or more or less omitted entirely in many introductory taxonomy courses. As the editor's introduction states, it serves to fill a place that was previously empty for the English reader.

In the final analysis, it combines the remnants of the out-worn system of Engler and Prantl with a modern re-interpretation of the Besseyan system. Like the phoenix arising from its ashes, it recreates in the light of modern knowledge another stage in the ever continuing search for the best system to reflect the evolutionary history of the angiosperms.

James W. Walker
GRAY HERBARIUM
HARVARD UNIVERSITY 02138

BIOGRAPHY OF THOMAS NUTTALL; A REVIEW WITH BIBLIOGRAPHY[1,2]

RONALD L. STUCKEY

Thomas Nuttall (1786-1859) is frequently regarded as one of North America's most important, widely traveled, pioneer naturalists. Miss Graustein's full-length biography presents for the first time in scholarly detail the career of this brilliant naturalist, born in Yorkshire, England, who at the age of 22 emigrated to Philadelphia to begin his scientific explorations. These travels through the Old Northwest, up the Missouri River, down the Mississippi River, through southeastern United States, down the Ohio River, up the Arkansas River, across the Rocky Mountains, down the Columbia River, over to Hawaii, and into southern California are discussed at length and mapped. His physical hardships in the American wilderness, vivid descriptions of frontier scenes and living conditions of the peoples, personalities of the companions with whom he sometimes traveled, information about many of the plants he collected and described, and the geological and archaeological phenomena he observed are all presented in great detail.

Although it may be inferred from the title that this book treats only Nuttall's travels in America, the contrary is the case, for the author adds considerable information on his family affairs, his several visits to England, and his horticultural pursuits in England during his later life. In addition, major portions of five chapters deal with his 11 years at Harvard University, a chapter in his life previously little known. For a man who left scattered on two continents bits and pieces of information concerning his personal life in letters, itineraries, travel narratives, or scientific papers and books, Miss Graustein has woven these facts remarkably effectively among the reports of his exploring

[1]*Thomas Nuttall Naturalist Explorations in America 1808-1841.* Jeannette E. Graustein. Harvard University Press, Cambridge. 481 pp. 1967. $11.95.

[2]Paper No. 746 from the Department of Botany, The Ohio State University, Columbus 43210.

expeditions. Through the book she frequently lets Nuttall speak for himself in many quotations from unpublished letters.

This biography also presents another look at the story of American botany during the period 1808-1841. Not only does the reader learn in detail about Nuttall's botanical pursuits in exploration and publication, but also about the many botanical friends and associates he had in America and England, perhaps the most important being William Baldwin, Benjamin Smith Barton, John Bradbury, Zaccheus Collins, William Gambel, Henry Muhlenberg, Charles Pickering, and Frederick Pursh. These naturalists provide much of the background against which the story of Nuttall's career is enacted. For American botanical historiography, this book is comparable to other biographies of American plant taxonomists, such as McAllister on Amos Eaton; Rodgers on William Starling Sullivant, John Torrey, John Merle Coulter, and Liberty Hyde Bailey; Dupree on Asa Gray; and Berkeley on John Clayton.

Of Nuttall's botanical associates, probably more new information is given on Zaccheus Collins than any of the others. As indicated in Miss Graustein's extensive footnotes, this information apears to be gleaned primarily from the numerous letters written to Collins now preserved in the library of The Academy of Natural Sciences, Philadelphia. At times, however, the source of the facts regarding Zaccheus Collins is not always presented. For example, on page 24, there is a quotation saying that Collins is "A retentive gulph . . ." without source, and on pages 272-273, the sale of Collins' Herbarium including dates, bidders, purchasers, and prices is given but not documented. The former item was probably quoted from Rev. L. D. von Schweinitz's April 19th, 1821, letter to John Torrey (Mem. Torrey Bot. Club **16**: 142. 1921) and the latter data were probably taken from Daniel Steinhauer's and C. S. Rafinesque's unpublished letters to Rev. L. D. von Schweinitz now in The Academy of Natural Sciences Library, Philadelphia.

There appear to be some inconsistencies in the use of scientific names of plants, especially in cases where Nuttall's names are no longer in use because of either subsequent taxonomic and/or nomenclatural changes. Citing later new combinations instead of the names of new species that Nuttall published is confusing. I point out the following items (in chapters 5 and 7) which pertain to Nuttall's plants from the 1810-1811 expedition in the Great Lakes region and Missouri River valley and from his 1816 trip in the Ohio River valley. Among a list of five of Nuttall's new species from the Mackinac Straits region mentioned on page 51, Miss Graustein includes *Cirsium undulatum* (Nutt.) Spreng. Actually this species was published by Nuttall as *Carduus undulatus* (Gen. 2: 130), but later transferred to *Cirsium* by Sprengel. Other instances of this kind of reporting occur on page 71 for *Opuntia fragilis* (Nutt.) Haw., actually *Cactus fragilis* (Gen. 1: 296), *Mamillaria vivipara* (Nutt.) Haw., actually *Cactus viviparus* (Gen 1: 295), *Lactuca ludoviviana* (Nutt.) Riddell, actually *Sonchus ludovicianus* Nutt. (Gen. 2: 125). In other instances, the author follows an accepted procedure by giving the recognized new combination or new name in square brackets following Nuttall's published name, for example, p. 37, *Hedeoma glabra* [*Satureja arkansana* (Nutt.) Briq.]; p. 98, *Enslenia albida* [*Ampelamus albidus* (Nutt.) Britt.]; p. 106, *Dracocephalum cordatum* [*Meehania cordata* (Nutt.) Britt.]; and p. 102 *Liatris corymbosa* [*Carphephorus corymbosus* (Nutt.) T. & G.].

Concerning some other records of plants mentioned in chapters 5 and 7, the following four cases are noteworthy:

(1) The author believes apparently without evidence that Nuttall omitted the *Euonymus* [*E. obovatus* Nutt.] from his 1810 diary (p. 45, footnote 8). Recent evidence suggests that Nuttall first found the *Euonymus* on his 1816 foray into western Pennsylvania (Mich. Bot. 6: 92-93. 1967).

(2) Miss Graustein states that Nuttall obtained his *Dalea enneandra* at Prairie du Chien (p. 54). This species

is described in *Fraser's Catalogue* without locality, but one would assume from the title of the catalogue that the plant came from somewhere in "Upper Louisiana" or on the "River Missourie." Pursh (Fl. Am. Sept. 2: 741. "1814" [1813]) described a *D. laxiflora* from "Upper Louisiana" based on a collection by Bradbury and seen in his herbarium. Pursh placed *D. enneandra* of *Fraser's Catalogue* in synonymy. In his *Genera* (2: 101), Nuttall recognized Pursh's *D. laxiflora* but not the *Fraser Catalogue D. enneandra.* Nuttall gave the localities as "On the high hills and naked grassy plains of the Missouri, also on the banks of the Mississippi near the Praire du Chien." Without further evidence one can only infer that Nuttall found the *D. enneandra* at the latter location. Nuttall's manner of treating the locality data suggests that this is another plant that he originally collected at Prairie du Chien, lost it, and recollected another one later in the Missouri region. This suggested interpretation of these data is consistent with my theory that Nuttall lost most of his plants on the 1810 trip, but still cited their localities in his *Genera* (Stuckey, Mich. Bot. 6: 81-94. 1967).

(3) The author says (p. 58) that "the species of poppy [*Stylophorum diphyllum* (Michx.) Nutt.] on which he [Nuttall] based his genus **Stylophorum*" came from "Near St. Louis." Although the locality may have been near St. Louis, Nuttall wrote, "In the shady woods of Kentucky and Tennessee, also on the banks of the Missouri;" (Gen. 2: 7). Unless the author has other uncited documentation, one should not read added information into the locality data Nuttall gave in his *Genera.*

(4) Concerning Nuttall's 1816 travels in the Ohio River valley (p. 106), Miss Graustein notes: "At Portsmouth he made a foray up the Scioto River where he saw *Juglans nigra* L." The reference given is Nuttall's *Sylva* I, p. 41, but I fail to find this plant mentioned on that page or any comment concerning a trip up the Scioto River. Perhaps this note appears in another reference unknown to me.

Miss Graustein believes that Nuttall's work in the *Genera*

was impaired because of his deficiency in taxonomic training (p. 121-122). Although that may be true, she supports her viewpoint by saying that Nuttall "remained oblivious to simple conventions such as the retention of the original specific name when transfer is made to a different genus." To state that Nuttall was ignorant of so simple a rule is completely unjustified. In Nuttall's day there was no *Code of Botanical Nomenclature*, but only the guidelines provided by Linnaeus' *Philosophia Botanica* and *Critica Botanica*. It was not until 1866, when the Botanical Congress commissioned Alphonse DeCandolle to draw up some "Laws . . . ," which were adopted by the Congress in 1867, that there was any written "rule" regarding retention of name on transfer (*see* C. A. Weatherby, Am. J. Bot. **36**: 5-7. 1949). Furthermore, it has not been until the present century that this procedure has been widely practiced.

On the whole, the book is well documented by notes occupying 54 pages, all placed at the back of the book. There is no concise alphabetically (by author) arranged list of consulted references, although a list of 15 papers concerned mostly with biographical sketches of Nuttall do appear on page 401. On pages 473-474 of the index there is a partial list (20 entries) of the titles only of Nuttall's own publications. A more complete list of 51 titles usually with pages, dates, and place of publication can be found in Smith and Thieret (Leafl. West. Bot. **9**: 33-42. 1959), an important reference not cited by Graustein. I believe Miss Graustein's biography, like some others in recent years concerned with botanists and perhaps with scientists in other fields, is deficient in its presentation or listing of the scientist's own published works. It seems to me that one of the minimum requirements of a biography would be the preparation of a complete chronologically arranged bibliography of the man or woman about whom an author is writing. In the botanical field, and especially in the area of plant taxonomy, where exact dates of publication are often extremely important in settling questions of priority of plant names, a bibliography including full title, publication date, volume

number, and page numbers accompanied by pertinent annotations, is essential. Usually this information can best be supplied by the biographer who is familiar with the many aspects and sequence of events of the scientist's life.

As part of my research on Thomas Nuttall's contributions to plant taxonomy, I have been accumulating biographical references, as well as papers that discuss taxonomic and nomenclatural problems of his plants, his itineraries, correspondence, and/or relationships with other botanists. Many of these references are useful to the plant taxonomist, but some of them are not cited by Graustein for various reasons. It seems desirable to include below a bibliography concerned with Nuttall, his plants, and plant exploration. This list is not intended to be complete, but represents those references gleaned primarily from journals on taxonomic botany.

Aside from the above criticisms of certain specific details, the student interested in biography, travel, and/or natural history in pioneer North America will find that this important book adds another rewarding chapter in those fields. Written for both the scholar and the layman, this book should appeal to a wide range of interests.

Publications about Thomas Nuttall and His Botanical Work
(Excluding Nuttall's Own Publications
in Smith and Thieret, 1959)

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DEPARTMENT OF BOTANY,
THE OHIO STATE UNIVERSITY, COLUMBUS 43210.

THE LINUM BAHAMENSE COMPLEX

C. M. Rogers[1]

Populations of flax, disjunct about 1000 miles from their nearest relatives in Mexico and western Texas, have been found on five of the Bahama Islands: Abaco, Andros, Eleuthera, Grand Bahama and New Providence. Small (1907) recognized four species. Recently (1963) I reduced these to one species, *L. bahamense,* with three varieties. One of these, var. *corallicola,* is conspicuously different in being densely pubescent throughout. The other two, var. *bahamense* and var. *bracei* are glabrous and were believed to be distinguished from one another by a series of more or less minor features. It was recognized, however, that, particularly on Grand Bahama, where the two varieties grow together, numerous intermediates could be found.

I have now had the opportunity to collect var. *bracei* from the type locality on Grand Bahama, var. *corallicola* from both Grand Bahama and Andros, and var. *bahamense* from Grand Bahama, Andros and New Providence; to grow them in the greenhouse; and to make a number of crosses.

All of the populations have been found to have a haploid number of 34 chromosomes. The basic number for the segment of the genus to which *L. bahamense* belongs is $n = 18$, so that the island populations are interpreted as aneuploid derivatives from an unknown tetraploid ancestor.

The differences in habit between var. *bracei* and var. *bahamense,* which appeared fairly marked on the comparatively few herbarium specimens previously available, disappear completely when these plants are grown together and, therefore, must be due to local environmental differences or season of collection. Crosses between the two are completely fertile and pairing at meiosis in the offspring is entirely normal. Not only are remaining minor differences between the two populations quite lost among the various greenhouse-grown plants and their offspring, but now a fairly large series of collections from Andros and New

[1]Contribution No. 199 from the Department of Biology, Wayne State University, Detroit, Michigan.

Providence Islands, where var. *bahamense* was thought to be the only entity, reveals "var. *bracei*" features intermixed. It seems unnecessary, if not impossible, to try to distinguish the two varieties and I propose that they be combined.

Until recently I knew of but three collections of var. *corallicola*, but, in 1965, I found that near San Andros, Andros Island, it was intermixed with the glabrous plant (var. *bahamense*) as a very common roadside weed. Crosses between a pubescent plant and several glabrous plants uniformly yielded only pubescent offspring. The hybrids are completely fertile and pairing of chromosomes at meiosis is entirely normal. Self-pollination of these F_1 plants give F_2 generation ratios of approximately 3 pubescent: 1 glabrous (74 plants examined). No plants intermediate in hairiness have appeared and it is quite clear that a very simple inheritance, probably a single gene controls this character. Therefore, in spite of the fact that pubescence is a very conspicuous feature, var. *corallicola* should be treated only as a form of *L. bahamense*.

When this is done, the complete synonymy for *L. bahamense* is then as follows:

Linum bahamense Northrop, Mem. Torr. Club **12**: 42. 1902.
forma **bahamense**.

Cathartolinum bahamense (Northrop) Small, North Amer. Flora **25**: 75. 1907.

Cathartolinum bracei Small, *loc. cit.* 1907.

Cathartolinum lignosum Small, *loc. cit.* 1907.

Linum lignosum (Small) Winkl. in Engl. & Prantl, Natürl. Pflanzenfam. ed. 2, 19a: 116. 1931.

Linum bracei (Small) Winkl. *loc. cit.* 1931.

Linum bahamense var. *bracei* (Small) Rogers, Brittonia **15**: 107. 1963.

Linum bahamense forma **corallicola** stat. nov.

Cathartolinum corallicola Small, North Amer. Flora **25**: 74. 1907.

Linum corallicola (Small) Winkl. in Engl. & Prantl, Natürl. Pflanzenfam. ed 2, 19a: 116. 1931.

Linum bahamense var. *corallicola* (Small) Rogers, Brittonia **15**: 107. 1963.

DEPARTMENT OF BIOLOGY
WAYNE STATE UNIVERSITY
DETROIT, MICHIGAN 48202

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SEASONAL OCCURRENCE AND ECOLOGY OF SALT MARSH PHANEROGAMS AT IPSWICH, MASSACHUSETTS[1]

E. E. WEBBER

For the past several years, research into the ecology and systematics of benthic algae has been in progress at a salt marsh adjacent to the Castle Neck River, Ipswich, Massachusetts. Because of the close association between many of these algae and the salt marsh seed plants, it was essential to characterize this salt marsh area as to its phanerogam vegetation. The present paper reports on the presence and distribution of the dominant seed plants characteristic of the Ipswich salt marsh.

Principal references used for species determinations were Gleason and Cronquist (1936), Mason (1957), and Fernald (1950). Specimens of the plants collected are deposited in the Herbarium, University of Massachusetts, Amherst.

The phanerogams collected as indicative of the Ipswich salt marsh and its immediate surroundings are as follows:

MONOCOTYLEDONAE

Ruppia maritima L.
Triglochin maritima L.
Eleocharis halophila Fern. & Brack.
Scirpus americanus Pers.
Juncus gerardi Loisel.
Bromus tectorum L.
Glyceria melicaria (Michx.) Hubb.
Distichlis spicata L.
Phragmites communis Trin.
Agropyron pungens (Pers.) R. & S.
Spartina pectinata Link
Spartina alterniflora var. *glabra* (Muhl.) Fern.
Spartina patens (Ait.) Muhl.
Panicum virgatum L.

[1]Modified from a section of a Ph.D. thesis, "Systematics and Ecology of Benthic Salt Marsh Algae at Ipswich, Massachusetts", submitted to the Gradrate Faculty, University of Massachusetts, Amherst.

DICOTYLEDONAE

Myrica pensylvanica Loisel.
Polygonum aviculare L. var. *littorale* (Link) Koch
Bassia hirsuta (L.) Aschers.
Atriplex patula var. *hastata* (L.) Gray
Salicornia bigelovii Torr.
Salicornia europaea L.
Suaeda maritima (L.) Dum.
Suaeda richii Fern.
Suaeda linearis (Ell.) Moq.
Spergularia marina (L.) Griseb.
Trifolium arvense L.
Hudsonia tomentosa Nutt.
Glaux maritima L.
Limonium nashii Small
Gerardia maritima Raf.
Plantago maritima L.
Solidago sempervirens L.
Aster sp.

SEASONAL DEVELOPMENT.

Two of the dominant species, *Juncus gerardi* and *Spartina patens,* began their growth period far earlier than the remainder of the marsh phanerogams. Young green shoots of these two species a few centimeters in height were collected from beneath the ice and snow covering the marsh in February, 1963 and 1964. By early May *Juncus gerardi* shoots had increased to 15 cm in height, while those of *Spartina patens* were 7 cm tall.

In contrast, emergent shoots (1-3 cm tall) of the following plants became apparent in early May throughout the marsh:

Glaux maritima
Eleocharis halophila
Plantago maritima
Atriplex patula var. *hastata*
Suaeda richii
Suaeda linearis
Limonium nashii

The first flowering of salt marsh phanerogams began in late May with *Glaux maritima, Eleocharis halopila,* and *Plantago maritima.* These were followed in June by *Juncus gerardi, Scripus americanus, Phragmites communis,* and *Ruppia maritima.* By July, *Spartina patens* and *Limonium nashii* joined the species already in bloom. The majority of seed plants flowered during August, among them the following:

Suaeda linearis	*Salicornia bigelovii*
Suaeda richii	*Salicornia europaea*
Spergularia marina	*Bassia hirsuta*

In September, the marsh appearance changed from a lush summer green to an autumn brown with splotches of yellow, purple, and red belonging to the blooms of *Solidago sempervirens, Aster sp.*, and the stems of *Salicornia sp.* respectively. Also in flower during September, but much less evident than the aforementioned autumn species, was *Gerardia maritima,* growing among the taller culmns of *Spartina patens* and the scapes of *Plantago maritima.*

DISCUSSION OF PHANEROGAM DISTRIBUTION.

Throughout the Ipswich marsh the phanerogam vegetation follows a recognizable pattern of distribution. In a landward direction the dominant species succeed each other in the following sequence: *Spartina alterniflora* var. *glabra*; *Spartina patens*; a mixture of *Spartina patens* and *Distichlis spicata* or, where the topography was sloping, a *Spartina patens* — *Scirpus americanus* mixture; and *Juncus gerardi.*

Historically, explanations of seed plant distribution in the salt marsh habitat have emphasized the importance of tide levels in conjunction with the ability of a particular species to tolerate varying concentrations of salt in the soil solution, as well as periods of tidal immersion.

Johnson & York (1915) related tide levels on Long Island marshes to seed plant zonation, and suggest that the upper and lower distributional limits for a particular plant are controlled by the ability of that plant to withstand specific periods of submergence and emergence. These authors also indicate that light availability may be involved in the maximum downshore extension of *S. alterniflora* var. *glabra,* a point recently reemphasized by Ranwell, et al. (1964).

On the Saugus marsh (Massachusetts), Chapman (1940) found the tidal factor to be ultimately the most important ecological variable in controlling phanerogam distribution.

Additional investigations of phanerogam distribution on other North American salt marshes indicate the importance of tide levels as they influence soil salinities and soil drainage (Penfound & Hathaway, 1939; Uphof, 1941; Purer, 1942; Reed, 1947; Hinde, 1954).

Results of culture experiments reported to date suggest that, in general, different salinity tolerance levels (Taylor, 1939) and specific nutrient requirements (Adams, 1963) of the various species are responsible for their zonation in salt marshes. An excellent review of pertinent physiological data attempting to explain, at least in part, the distribution of salt marsh seed plants has been presented by Chapman (1960).

At the Ipswich marsh I have recognized the importance of several factors related to phanerogam distribution, e.g., proximity to saline or fresh water influences, marsh surface topography, and character of the substrate.

The pioneer phanerogam to colonize the marsh was *Spartina alterniflora* var. *glabra*, forming a band of vegetation along marsh edges and creek margins. Its landward extent coincides with high water neap tide levels. Maximum vegetative and reproductive growth was restricted to those plants on the marsh near this level. At its lower limit, this species was only several centimeters tall and typically vegetative. The distribution of *S. alterniflora* var. *glabra* at Ipswich is confined to marsh areas with muddy substrate, poor drainage, repeated tidal inundation, and continual mud and silt deposition.

Above high water neap tide levels an extensive *Spartina patens* - *Distichlis spicata* mixture occurred on flat sections of the marsh which lacked even the slightest slope. In Connecticut, Nichols (1920) found that poorly drained marsh areas above high water neap tide levels were populated by *Distichlis spicata,* and with improved soil drainage *S. patens* became abundant. Taylor (1939) noted that *D. spicata* was more vigorous in growth and flowering at higher salinities in culture solutions. While Purer (1942)

has reported *D. spicata* to be typical of marsh sections having reduced salinities and improved aeration, Adams (1963) using nutrient solution experiments, has shown that *Distichlis* grows best in a saline medium. It may be that the flat and more fully exposed marsh areas at Ipswich had a higher soil salinity than sloping, better drained situations, thereby accounting for the characteristic distribution of *Distichlis spicata*.

The presence of a zone lacking vegetation, a "barren zone", was evident immediately landward to the *Juncus gerardi* consocies on the marsh adjacent to the Castle Neck River. The gently sloping character of the marsh here permitted the retention of tidal debris in this "barren zone". In their study of Connecticut tidal marshes, Miller and Egler (1950) noted that tidal trash in the upper *Juncus gerardi* consocies commonly killed the plants which it covered. At Ipswich the mass of debris, with its accompanying high temperatures and poor air circulation, very likely had a similar effect on a potential vegetation becoming established in this zone. Perhaps high temperatures beneath this debris resulted in excessive salinity, both factors acting to prevent the establishment of seedlings.

A tidal creek at the head end of the marsh was the sole habitat for *Ruppia maritima*, where the plants, anchored in the soft mud of the creek bed, undoubtedly aid in stabilizing this substrate. The plants were never exposed during periods of low tides; indeed, *Ruppia* is unable to withstand exposure to the desiccating effects of sun and air (Chapman, 1960). Citations are common indicating the restricted distribution of *R. maritima* to "brackish water" areas, without specifying salinity readings. An early account of the response of *R. maritima* to varying salinities was made by Graves (in Harshburger, 1909) who found cells of *Ruppia* to tolerate salinities to 25°/oo, but to plasmolyze in salinities of 30°/oo. Maximum growth and development of *Ruppia maritima* at Ipswich was related to a summer salinity range of 20-25°/oo (once to 27°/oo).

Equally distinctive and more characteristic as a salt marsh phanerogam is the genus *Salicornia*. Its brilliant scarlet autumn coloration together with its clonal distribution on the marsh signify "salt marsh" to the observer. Species of *Salicornia* have long been recognized as true halophytes. Halket (1915) and Taylor (1939) have shown experimentally that this plant grows best in 2-3% NaCl solutions. Numerous additional reports pertaining to the halophytic character of the various species of *Salicornia* are contained in Chapman (1960). For the Bay of Fundy marshes (Ganong, 1903), *S. stricta* is typically one of the first phanerogams to colonize eroded segments of the marsh, and for New England marshes, a Salicornetum characteristically develops on bare mud, where high salinities would be encountered (Chapman, 1960). At Ipswich, *Salicornia bigelovii* was abundant in the more poorly drained sections of the marsh, and where the plants were entirely submerged during high water spring tide levels. In contrast, *Salicornia europaea* was always limited to the better drained areas, e.g., as scattered plants along the lower edge of the Spartinetum patentis. However, in several marsh depressions at the head of the marsh *S. europaea* was often the sole component. While soil salinities were not determined for those marsh areas with *S. bigelovii* and *S. europaea*, the proximity to fresh water influence and the greater retention of rain water in the depressions at the head of the marsh, may have produced a less saline environment more conducive to the development of *S. europaea*.

Seed dissemination and germination for the salt marsh annuals is an area of investigation which has progressed little beyond a general consideration of but a few species. During his study of the Saugus marsh, Chapman (1940) noted that seed germination of the annual species occurred in the spring, when the salinity level of the soil surface layers was low. In laboratory experiments he showed that maximum germination of several species occurred in fresh water, although optimum germination for *Salicornia bigelovii* from Saugus (Massachusetts) required a 1% NaCl

solution. He also demonstrated that freezing temperatures interact with salinity levels in affecting seed germination of *S. bigelovii*, for while the per cent germination decreased with increasing salinities, this was partially offset by lower temperatures.

In contrast to *Salicornia*, seeds of *Plantago maritima* germinate best in fresh water (Chapman, 1940). At Ipswich *Plantago maritima* and *Glaux maritima* appeared in early May, their seeds apparently germinating when the salinity of the marsh surface soil would be expected to be lowest.

Another consideration relating to salinity and seed plant growth pertains to changing salinity levels as the plants age. Turner (in Chapman, 1960) has shown that *Suaeda novae-zelandiae* grows best in a 1% NaCl solution during its early stages, but that when the plants are six months old, a 3% NaCl solution yields maximum growth and development. It is clear that while salinity levels are important in the germination of some salt marsh annuals, one must also consider salt concentrations of the soil solution throughout the growing season as the plants develop. The distribution of *Suaeda (maritima, linearis, richii)* at Ipswich occurred in the upper marsh levels, as scattered plants among *Spartina patens* or, occasionally, at the upper boundary of *Juncus gerardi*. Seed germination of *Suaeda maritima* is best in fresh water, although the per cent germination is very small (4%); however, another species, *S. novae-zelandiae*, has an optimum of 41% in fresh water (Chapman, 1960). Germination of *Suaeda* seeds at the higher marsh levels at Ipswich may be related to low soil salinities which probably exist here during the early spring.

Atriplex patula var. *hastata* also occurs with *Suaeda* at these higher marsh levels. Seed germination in *Atriplex* is inhibited by the high chloride content of sheathing bracteoles, for removal of these bracteoles results in immediate germination (Beadle, 1952). At the higher marsh levels,

the chloride concentation of *Atriplex* bracteoles could be reduced readily by spring rains, resulting in early spring germination which was observed for this species at Ipswich.

It is immediately evident that continued research is necessary with the salt marsh phanerogams to define their specific growth requirements, and therefore more accurately interpret their distribution in salt marshes. Additional and detailed field studies coupled with laboratory experiments should be initiated with this view in mind.

DEPARTMENT OF BIOLOGY
KEUKA COLLEGE
KEUKA PARK, NEW YORK

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SPOROBOLUS TEXANUS VASEY IN LINCOLN, NEBRASKA

Sporobolus texanus was collected in saline soils in Lincoln, Nebraska on July 7, 1965, *Ungar 1190* (KANU), and August 28, 1967, *Ungar 1231* (Ohio University Herbarium). This is the northeasternmost extension of the range of this species. It is about 70 miles east and 80 miles north of any previously reported collection of *S. texanus.*

Prior to this collection, the most northern and eastern collection had been reported by Gates (1940) for Cloud County, Kansas, which is in northcentral Kansas. According to Hitchcock (1950) *S. texanus* is primarily a southwestern species, occurring in Kansas, Oklahoma, Texas, Colorado, Arizona, and New Mexico. It occurs in non-saline prairie soils, prairie bordering saline marshes, and is occasionally an invader of open salt flats from Oklahoma north to Lincoln, Nebraska (Ungar, 1965, 1966, 1967).

S. texanus occurs in two communities in the Lincoln marsh area on the south side of Highway 6-2, opposite 720

west 0 street. In one area which is slightly saline, 0.45% to 0.70% salt on a dry weight basis, it is associated with *Hordeum jubatum* L., *Iva annua* L., *Distichlis stricta* (Torr.) Rydb., *Poa arida* Vasey, *Agropyron smithii* Rydb., *Melilotus officinale* Desr., *Atriplex patula* L. var. *hastata* (L.) Gray, and *Rumex crispus* L. It also occurs rarely in highly saline soils, 0.61% to 2.2%, invading a salt pan occupied by the highly salt tolerant *Suaeda depressa* (Pursh) Wats., *Salicornia rubra* Nels., and *Distichlis stricta*. Its range of salt tolerance appears to be very broad and it has been found in soils ranging from 0.003% to 2.5% salinity (Ungar, 1965, 1966).

The possibility of *S. texanus* occurring in saline soils which are still farther north in South Dakota and North Dakota are being investigated. Field work in 1967 in saline areas of Codington County and Day County, South Dakota indicates that *S. texanus* is not found in these areas though the remaining vegetation complement is similar to the Lincoln, Nebraska marshes.

IRWIN A. UNGAR[1]
BOTANY DEPARTMENT
OHIO UNIVERSITY, ATHENS 45701

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RANGE EXTENSION OF MUHLENBERGIA SOBOLIFERA IN NEW HAMPSHIRE

The collection of *Muhlenbergia sobolifera* (Muhl.) Trin. proved to be the most significant record of a two year floristic study conducted on Rattlesnake Island, East Alton, New Hampshire.[1] This was the first record for Belknap County and the second record for the state. The previous record was by A. A. Eaton in Nottingham, September 1899.

The collection was obtained below a shaded ledge on the south facing talus slope. Significant species occurring on the same slope include: *Asplenium platyneuron*, *Hystrix patula* var. *Bigeloviana*, *Silene antirrhina*, *Arabis Drummondii*, *A. missouriensis*, *Ceanothus americanus*, *Prunus susquehanae*, *Specularia perfoliata*, and *Carya ovata*.

This talus slope rising some 400 vertical feet from the lake's surface, resembled closely in species composition a similar talus slope in the Pawtuckaway Mountains, Nottingham, New Hampshire. The slope at Rattlesnake Island is believed to be of the same geologic origin as the Ossipee Mountains some 20 miles to the north and west. Collections are to be placed in the herbarium of the New England Botanical Club, Cambridge, and the University of New Hampshire Herbarium in Durham.

WENDELL H. BERRY, JR.[1]
LAKE FOREST ACADEMY
LAKE FOREST, ILLINOIS 60045

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[1]Thesis research conducted from 1964-66 under the direction of Dr. A. R. Hodgdon.

A NEW FORM OF MYRICA PENSYLVANICA

While collecting in the Ocean Park section of Old Orchard Beach, York County, Maine, in the summer of 1967, I noticed that certain bayberry plants were conspicuous for their extremely small leaves. The fruit were also impressively smaller than on typical plants. Such aberrant plants were often found beside typical plants, but no plants with intermediate characters were found. About 5% of the Ocean Park bayberry plants are of this new form. All the bayberry plants in Ocean Park are found in open sandy soil within ½-mile of the beach.

Myrica pensylvanica Loisel. forma **parvifolia** T. W. Wells, forma nova. Type Specimen: T. W. Wells, Old Orchard Beach, York Co., Maine, 5 Sept., 1967 (N.E.B.C.).

Differt a forma typica foliis multo minoribus maturisque baccis minoribus: foliis ad 3½ cm longis, ad 1½ cm latis; maturis baccis ad 3.5 mm latis.

The difference between this form and forma *pensylvanica* is in the much smaller size of the leaves and fruit: the larger leaves up to 3½ cm long and 1½ cm wide, but averaging under 3 cm long and under 1 cm wide; and the mature fruit up to 3.5 mm in diameter.

Voucher specimens are deposited in the herbarium of the New England Botanical Club.

THEODORE W. WELLS
MILTON ACADEMY
MILTON, MASSACHUSETTS 02186

A YELLOW-CENTERED FORM OF HELENIUM NUDIFLORUM

This form was found growing on the western shore of Hinckley Lake near the mouth of Beaver Meadow Creek, about one mile north of Hinckley, New York. It was growing in close association with the typical form (with brown or purplish disk) and was widely, though sparingly, distributed through the community. It was observed by myself and by Stanley J. Smith, during the 1966 season and again in 1967. It was collected in August, just as the disc flowers were beginning to open (No. *3231* in the Oneida County collection at Utica College of Syracuse University, Utica, New York) and in September, at which time the ovules were plump and well-developed (No. *3246*). Mr. Smith also collected this form and added it to the collection in the state herbarium in Albany. (No. *40666, S. J. Smith* and *T. C. Baim*)

It is suggested that this form be named *Helenium nudiflorum* forma *homochromum* Howe, forma nova: Differt forma typica floribus tubulosis luteis.

Type in the Herbarium of Utica College of Syracuse University, Oneida County Collection, *Howe 3246.*

M. DORISSE HOWE
DEPARTMENT OF BIOLOGY
UTICA COLLEGE OF SYRACUSE UNIVERSITY
UTICA, NEW YORK 13502

TWO EUPATORIUM SPECIES NEW TO CONNECTICUT. Although usually warned by signs against trespassing, it may be found by one who does so that railroad rights-of-way, yards, and terminals are good places to botanize with the hope of finding plants from distant parts which are new to one's area. That conclusion is supported by the following incidents.

In 1963 while riding down a sandy lane toward sand-pits in North Haven, Connecticut, I caught sight of a beautiful tall whitish-flowered plant with strongly 3-veined leaves, which proved to be the Tall Thoroughwort, *Eupatorium altissimum* L. Upon botanizing the area, I discovered that on both sides of the railroad tracks there were many plants of this species intermingled with *Eupatorium hyssopifolium* L. Since that time, although one large area has been destroyed by the parking of trucks and tractors of the Connecticut Highway Dept., the species is rapidly spreading over a large area. Gray's Manual gives the range of the species as Pennsylvania, westward and southward.

Recently, while driving through the Brewery St. yards at the New Haven Railroad repair shops, I noticed another tall whitish-flowered composite. This one turns out to be *Eupatorium serotinum* Michx., the range of which, according to Gray's Manual, is north to New Jersey and adventive in Massachusetts. It is described in the Manual as "somewhat aggressive and weedy," and in this locality it certainly deserves that reputation, as there are scores of plants singly and in clumps scattered over several acres.

It may be expected that both of these species are spread by association with the railroad, either "hitch-hiking" on equipment or by suction from passing trains. They should be watched for in other areas.

Specimens of each are deposited in the Herbaria of Yale University, the University of Connecticut, Pringle Herbarium of the University of Vermont, and the herbarium of the New England Botanical Club at Harvard University.

JAMES J. NEALE
39 FAIRMOUNT AVENUE
NEW HAVEN, CONNECTICUT 06513

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Rhodora

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 70 October-December No. 784

JOHN GOLDIE AND THE REPUBLICATION OF HIS DIARY

Joseph Ewan

John Goldie (1793-1886) is remembered by users of Gray's *Manual* through the tallest and largest of Wood ferns, *Dryopteris goldiana* (Hook.) Gray *(Aspidium goldianum)*, but few know his *Diary* published in 1897 in Toronto in a small privately printed edition. In the course of restoring materials in the Toronto Public Library, the Philadelphia artisan-bibliographer, Willman Spawn, discovered that the manuscript from which the 1897 printing was made differed from the published version and urged Goldie's granddaughter, Mrs. Theresa Goldie Falkner, to reissue the *Diary, verbatim et literatim.* It appeared December 6, 1967[1] with an introduction and thirty-six superscriptoral notes. To report factually, the notes which Mr. Spawn had so carefully prepared were drastically abbreviated and he did not see proofs before publication. Yet the *Diary* is now available for the first time as written by John Goldie, attractively bound in stiff-paper cover with a frontispiece portrait, and two pages reproduced from manuscript. Apart from its intrinsic botanical interest it will be a sought-for Americana item. We are grateful to Mrs. Falkner and Willman Spawn for their contribution to American botany.

[1]*Dairy of a Journal through Upper Canada and some of the New England States, 1819.* John Goldie. [Toronto, 1967] x + 65 pp. portr. frontis. May be purchased from University of Toronto Bookstore, $1.75 net.

The plate of "Aspidium goldianum" and the "original description" (pp. 64-65) are not satisfactorily identified. The plate reproduced here is Faxon's made for Daniel Cady Eaton's *Ferns of North America* (pl. XL) drawn from a Vermont specimen. The "original description" of *Aspidium goldianum* Hooker was published by Goldie in the *Edinburgh Philosophical Journal* in 1822. A map locating Goldie's place names would have been welcome, but the two examples of his handwriting will be useful in verifying labels encountered in herbaria. Goldie was not mentioned in *Index Herbariorum, Collectors* Part II (2) 1957. In addition to specimens at Kew about twenty Goldie specimens are preserved in the original Fielding Collection in the Oxford University Herbarium according to Hermia Clokie, *An Account of the Herbaria of the Department of Botany in the University of Oxford* (1964).

Fate dealt harshly with Goldie who came to America in 1817 on the advice of William Jackson Hooker of Glasgow whose enthusiasms for field collecting are well known. On three separate occasions Goldie lost his plant specimens in transit between Canada or New York and England. The loss of his botanical journal describing his collections made in Newfoundland, Quebec, Ontario, New York, and New Jersey, was an immediate tragedy to Goldie for it wiped out recognition of possible discoveries that might have been credited to him, and a permanent loss to us were the records of native vegetation which covered what today are, as Spawn observes, "housing developments, industrial parks, shopping centers and all the manifestations of urban sprawl." This surviving *Diary* is a fortunate reminder "of a land and a time we have left behind."

Biographical notices of Goldie have been liberally published and are listed below. Most of these are based on the autobiographical sketch which appeared in 1822. Almost wholly neglected is Goldie's own list of his American introductions and "observations" thereon (1827), brought to print by the zealot in horticultural publishing, John Claudius Loudon. But none of these accounts, largely repetitive, quote the two letters from Goldie to his professor extraordi-

nary, William Jackson Hooker, preserved at Kew. These are here published through the genial courtesy of Sir George Taylor. The first letter records his association with James McNab and his botanizing in Russia; his second was written from "Canada West" whither he immigrated to a farm "about a mile from Ayr, in the county of Waterloo," his new Scotland.

"Wrightfield, June 16, 1837

Dear Sir

I have been called upon by a medical student, Mr. Paton from Air, who stated that if he obtained a recommendation from any of your acquaintances he would be permitted to attend your Botanical Class: with regard to which, I beg leave to say, that although not very intimately acquainted with him, yet I believe him to be very deserving of encouragement in his studies. He has always sustained an excellent character; and his Mother who is a Widow, having lost her husband at sea, has by industry and economy, been able to support herself and family respectably: yet not able, without a great sacrifice, to afford her son the means requisite for the completion of his studies in the profession which he intends to pursue. He seems exceedingly anxious to attend the Botanical Class, and should you be as kind as [to] give him a ticket, I feel assured that it will be received with much gratitude. My Friend, Mr. James McNab[2] visited me the other day, and I expect to see him again to night on his way home. I am going to send by him a sketch of an Iris which I brought from St. Petersburgh in 1830. It flowered last year but I am sorry to say that I have nearly lost the plant. The flower was very singular and very beautiful. The drawing was taken by a Lady; but it is not a good likeness of the flower. Mr. McNab will give more minute information. I would feel much gratified by having the name of the species. Should the plant live and flower with me again I will send you a specimen —

I am
Dear Sir
Your Honoura'
Obedt Sert.
John Goldie

---

[2]James McNab (1810-1878) had visited New Jersey, Pennsylvania, and Richmond, Virginia, in 1834, and was to succeed his father William McNab (1780-1848) as Curator of the Edinburgh Botanic Garden in 1849

II

Ayr, Canada West
Sept 2nd 1851

Dear Sir William,

I am afraid that you will have forgotten me altogether. A very excellent young man from this quarter is going out to Jamaica as a missionary, and as he wishes to see through the Kew Gardens requested an introduction to you. My Friend, Mr. Scott, is very fond of plants, and knows all that is interesting in this vicinity.

I have now been located, as the Yankees say, in this place for the last seven years and am likely to remain here during life. There are many interesting plants in the neighbourhood, several of which I cannot make out from Pursh,[3] and I have no other scientific work except Nuttall's Genera. I am sorry that I had no knowledge of Mr. Scott's going to London untill very lately else I would have had some specimens prepared to send you of such things as I could not make out satisfactorily.

I have bought a piece of land which I occupy as a farm, and have lately erected a Flour Mill, which has taken both my time and money and has prevented me from travelling so much as I would like to do. I have never been many miles from home except at N. York.

I found lately some of the *Gerardia quercifolia*,[4] a beautiful plant. *Batschia canescens*[5] is also fine, but very local, it is only in a few places that it is to be found. Mr. Scott found the *Batschia longiflora*[6] near Toronto.

You must now have a splendid collection in the Kew Gardens, and I feel glad that the public are admitted to admire them.[7]

There is one of my sons in N. Jersey, who has taken a fancy for entomology, and who has made a good collection,[8] but is greatly at a loss for a descriptive work on American Insects. If you will have the kindness to write to me, and state what may be the best work on the subject, I would feel greatly obliged — Would American Insects

---

[3]Frederick Pursh, *Flora Americae Septentrionalis* (London, 1814), 2 vols.

[4]*Gerardia flava* L.

[5]*Lithospermum canescens* (Michx.) Lehm.

[6]*Lithospermum incisum* Lehm.

[7]P. H. Gosse's *Wanderings through the Conservatories at Kew* (London, [1856]) offers an excellent commentary on Hooker's achievement.

[8]Judging from entomological rosters and history consulted, Walter Horn and Ilse Kahle (1935-36), Mathilde M. Carpenter (1945), and Harry B. Weiss (1936), the son's insect specimens did not survive.

sell in London? A letter from you would afford much gratification. I shall never forget your kindness. I feel confident that you will show my Friend all your rarities, and remain, Dear Sir W.

yours sincerely

John Goldie

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Hooker wrote to John Torrey, 29 May 1823, regarding Torrey's opinions on Goldie's paper of the previous year (A. D. Rodgers III, *John Torrey,* 1942, 58)

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A CASE OF MISTAKEN IDENTITY, OR THE MYSTERIOUS C. E. LLOYD

Irving W. Knobloch

One of the most interesting travelogues dealing with the natural history of the New World is "Unknown Mexico", a two volume work by Carl Lumholtz (1902). In this account will be found those discoveries noted by him on a series of expeditions mostly in western Mexico during the years 1890 to 1898, a span of time interrupted from time to time for the purpose of raising money for further exploration.

About one and a half years were spent by members of the expedition among the unique Tarahumare Indians of Chihuahua, a group of cave-dwellers. Incidentally, Carl Lumholtz was born at Faberg, Norway in 1851 and died at Saranac Lake, New York on May 5, 1922.

In this offering we are only concerned with the first Lumholtz Expedition. From reading "Unknown Mexico" one gathers the impression that this lasted from 1890 to 1893 but others believe that the dates were 1890 to 1892. For example, J. A. Allen (1893) published a list of mammals and birds collected in northeastern Sonora and northwestern Chihuahua, Mexico on the Lumholtz Archaeological Expedition, 1890-1892. It is difficult to see how this article could have gotten into print in 1893 if the expedition did not end sometime in 1892.

According to Allen, the first expedition left Bisbee, Arizona in September 1890. It traveled 225 miles south to Bacadehuachy and Nacory on the Río Yaqui, passing San Pedro (32 miles south of Bisbee), Los Trincheras, Santa Barbera, Fronteras, Cachuta (102 miles south of Bisbee), Los Trinitas (127 miles south of Bisbee), Los Pinitos, Los Cuevas, Oputo, Granados, Bacadehuachyl (the last three on the Río Yaqui), thence eastward toward and across the Sierra Madre, passing the following — Nacory (3400 ft.), Heurachi (4000 ft.), Napolera, El Puerto (6300 ft.) Bavispe River, Rancho de Los Apaches (6620 ft.), Chuhuachupa, Tachico (2000 ft.) to San Diego (4000 ft.) on the eastern slope. From February 15th to March 1st trips were

made from San Diego to Guanopa, Río Chico and Tatuara. This itinerary evidently only encompasses the immediate time span during which F. Robinette of Washington, D.C. and A. D. Meeds of Minneapolis, Minnesota collected mammals and birds. It should be mentioned that the personnel of the expeditions changed often and that as many as thirty men were involved with the various Lumholtz expeditions.

Of course, botanists also accompanied Lumholtz. Several years ago, in doing the biography of all collectors of plants in northern Mexico (unpubl.), we became aware that the names of two botanists, C. E. Lloyd and C. V. Hartman were printed on several hundred (?) labels in various herbaria, as being the collectors of plants on the first Lumholtz expedition.

No problem presented itself in the case of Carl Vilhelm Hartman who was born in Orebro, Sweden on August 19, 1862 and who died in Stockholm, Sweden on June 19, 1941. We will pass over his illustrious history because it is not germane to our thesis. When we came to the collection of data on C. E. Lloyd, we located absolutely nothing regarding his background. The only major clue we found attesting to his existence is the printed herbarium labels, prepared at Harvard University by B. L. Robinson and M. L. Fernald. We frequently did encounter the name "Francis E. Lloyd." The latter, an eminent botanist, led a life which, in part, is difficult to put down upon an accurate time table. He was born in 1868 in England and entered Princeton University in 1889 as a junior, presumably having attended Lafayette College before this event. He terminated his undergraduate work at Princeton with graduation in 1891. Certain plant collections by him on the Lumholtz expedition are dated "1890", and it is possible, therefore, that he went to Mexico while still an undergraduate. This matter will be dealt with in more detail later. Lloyd was appointed a Fellow at Princeton 1891-2 but resigned presumably to take a position as assistant professor at Williams College. In 1895 he received an A.M. degree from Princeton. This year coincides with his tenure at Pacific University (1892 to 1897) but his A.M. degree may have been conferred *in*

absentia. Another overlap is found in the dates 1896 to 1906 when he was associated with the Teachers College at Columbia University. Lloyd received honorary Doctor of Science degrees from University of Wales and from the University of Masaryk. After 1906, his other employers were the Desert Laboratory of Carnegie Institute, the Continental Mexican Rubber Company, Alabama Polytechnic Institute and, lastly, McGill University in Canada. The above information was gleaned from various sources (Ridge 1968, Gibbs 1968, Scarth 1948, Wulf 1967, Thomas 1967, Mason 1958, Tryon 1959, Norwegian Embassy 1958, Schwarten 1959, Rollins 1958).

At this point, it seemed obvious to us that we had to choose between C. E. Lloyd and F. E. Lloyd. Accordingly we set down the following facts both pro and con.

Pro C. E. Lloyd

As stated above, the herbarium labels of the first expedition include a "C. E. Lloyd".

In the Preface to volume 1, page X of "Unknown Mexico" by Carl Lumholtz (1902), we find the statement "Messrs. C. V. Hartman and C. E. Lloyd were the botanists,".

A research article by B. L. Robinson and M. L. Fernald (1895) is entitled "New Plants Collected by Messrs. C. V. Hartman and C. E. Lloyd upon an archaeological expedition to northwestern Mexico under the direction of Dr. Carl Lumholtz".

One of F. E. Lloyd's closest friends was C. E. Bradley, research associate in chemistry at California Institute of Technology. Bradley correctly pointed out that F. E. Lloyd taught at Pacific University, Forest Grove, Oregon from 1892 to 1897. He does not believe that Lloyd went to Mexico until 1907. Since the first Lumholtz expedition was from 1890 to 1892, it would appear that either Francis E. Lloyd did *not* go on the trip, or, he left the expedition early to take the position at Pacific University in 1892.

Pro F. E. Lloyd

Paul Standley (1920) mentioned the name of F. E. Lloyd as being on the Lumholtz expedition.

The first Lumholtz trip was from 1890 to 1892. Dr. Francis E. Lloyd, having been born in 1868, was 22 years old at the time of the expedition and thus could very well have been on the trip.

Both the Barnhart File at the New York Botanical Garden and American Men of Science, 1944, indicate that F. E. Lloyd was on the Lumholtz expedition.

Dr. F. Shreve and Dr. F. E. Lloyd were well-known to each other, both having been on the staff of the Desert Laboratory in Arizona. In the Foreword to Dr. Howard Gentry's "Rio Mayo Plants" (1942), Dr. Shreve mentioned that C. V. Hartman and F. E. Lloyd accompanied Dr. Lumholtz on his 1890 expedition, an endorsement which can hardly be in error.

In M. L. Fernald's "Synopsis of the Mexican and Central American Species of *Alnus*" (1904) we note that *Alnus oblongifolia* Torr. was collected at Huehuerachi, Sonora at an altitude of 1230 meters in December 1890 by C. V. Hartman (no. 322) and by F. E. Lloyd (no. 464). In the same year F. E. Lloyd collected *Salvia elegans sonoriensis* at Rinconardo, Sonora, twenty-one days after Hartman collected the same taxon at Huehuerachi, Sonara (M. L. Fernald 1900).

Notholaena lumholtzii was collected by Hartman, number 298 (GH, US) on the Lumholtz expedition and is the type. Dr. F. E. Lloyd evidently collected the same species (no. 489) on the same trip. This specimen is also at the Gray Herbarium.

Dr. Carl Lumholtz (1891) himself mentioned Francis E. Lloyd as one of his collectors on page 389 of "Report on Explorations in Northern Mexico". This contradicts what he wrote in "Unknown Mexico" in 1902 but can be attributed to an excusable *lapsus mentis.*

When all the evidence given above is evaluated, it would seem logical to assume that one of the botanists on the first Lumholtz expedition was Francis E. Lloyd and not the mysterious "C. E. Lloyd". Since Francis E. Lloyd did not graduate from Princeton until 1891, and since some of his collections were dated 1890, we shall be forced to conclude

that Lloyd was still an undergraduate at the time of his participation in the Lumholtz adventure.

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
MICHIGAN STATE UNIVERSITY, LANSING

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HYBRIDIZATION WITHIN THE TRITICEAE OF ALASKA: A NEW × ELYHORDEUM AND COMMENTS.

Wm. W. Mitchell[1] and H. J. Hodgson[2]

Frequent intergeneric hybridization between members of the Triticeae has led some taxonomists to reconsider generic affiliations in this group. Löve and Löve (1965) recently included in the genus *Elymus* the members of *Agropyron* referred to *Roegneria* by some authors, at the same time transferring *Elymus arenarius* L. and its relatives from *Elymus* to *Leymus*. A number of these grasses occur in Alaska, and their crossing relations are pertinent to the proposed taxonomic realignment. This paper reports on an additional intergeneric cross in the Triticeae, summarizes the recorded crosses involving Alaskan Triticeae, and comments on the above realignment.

Plants found at two locations in the vicinity of Palmer, Alaska, are apparent hybrids of *Elymus sibiricus* L. and *Hordeum jubatum* L. The inflorescence of the hybrid has the general appearance of *H. jubatum* but is more nodding with shorter awns that become curved and divergent upon drying. The nodding habit of the inflorescence is not as extreme, however, as in *E. sibiricus* (Fig. 1). Under favorable growing conditions the plant is broadly tussocked and leafy and produces numerous flowering culms.

The characteristics of *Hordeum* are expressed in the possession of (i) 3 spikelets at a node, the laterals being subsessile, (ii) awnlike glumes, and (iii) a tendency to disarticulation of the main rachis. The *Elymus* influence is evident in a plurality of well-developed florets in all 3 spikelets on some of the plants and the occurrence of 3 spikelets at a node (instead of 1 or 2, which is characteristic of the × *Agrohordeum* hybrids).

---

[1]University of Alaska Agricultural Experiment Station, Palmer.
[2]Cooperative State Research Service, U. S. Department of Agriculture, Washington, D.C.

Plate 1398.

Fig. 1. *Elymus sibiricus* left, × *Elyhordeum arcuatum* center, *Hordeum jubatum* right.

The only wild ryes occurring in the area of hybridization are *Elymus sibiricus* and *E. mollis* Trin. *Elymus mollis* is essentially precluded from consideration because of its stiffly erect inflorescence, densely pilose glumes and lemmas, pilose rachis, large awnless spikelets, long anthers and strongly rhizomatous habit. The tufted *E. sibiricus* with its pendulous spike, long curved awns, scabrid spikelets, and spikelet measurements appropriate to the hybrid, quite obviously is one of the parents.

Both the long-awned *Hordeum jubatum* and short-awned *H. brachyantherum* Nevski occur in the area and possess characters pertinent to the hybrid. Some characteristics of the taxa under consideration are compared in Table 1.

Conceivably, either species of *Hordeum* could have combined with *E. sibiricus* to produce the hybrid. However, the long-barbed prickes and pilose leaf surface of the hybrid definitely favor *H. jubatum* over *H. brachyantherum*. Moreover, anther length of the hybrid tends to be intermediate between those of *H. jubatum* and *E. sibiricus*.

CYTOLOGICAL OBSERVATIONS.

The results of meiotic studies are summarized in Table 2. Both parents and the hybrid are tetraploids ($2n=28$).

TABLE 1.

Some morphological comparisons of × *Elyhordeum arcuatum* and its possible parents

	Hordeum brachy-antherum	Hordeum jubatum	× Elyhordeum arcuatum	Elymus sibiricus
lemma (mm)	6.5-10	5-7.5	9-11	9.5-14.2
lemma-awn (mm)	6-15	35-75	17-25	11.5-31
anther (mm)	1.3-1.8	0.8-1.4	1.0-1.5	1.4-1.9
abaxial surface of flag leaf	glabrous	often pilose	pilose	glabrous to pilose
abaxial surface of flag leaf	with scattered, short-barbed prickles	densely scabrid with long-barbed prickles	scabrid with short to long-barbed prickles	smooth to scabrid with short-barbed prickles

All cells viewed bore univalents varying in number up to 14. Generally 5 to 8 bivalents were present in a cell, and about one-half of the cells contained multivalents. Anaphase I figures contained from 7 to 16 laggards, and all 242 quartets observed bore micronuclei. The frequency of pairing and multivalent formation indicates some homology between one set of genomes as well as the occurrence of translocations in the differentiation of the genomes. Pollen

TABLE 2.

Observations of meiosis in × *Elyhordeum arcuatum*

Stage of Meiosis	No. Cells Observed	Univalents	Bivalents	Multivalents	Laggards
Metaphase I	23	245	126	11	
Anaphase I	24				311
Average per cell		10.7	5.5	0.5	12.7

grains accepted a light stain in aniline blue but not the deep granular stain of normal pollen. The hybrid appears completely sterile.

DESCRIPTION OF HYBRID.

× **Elyhordeum arcuatum** Mitchell & Hodgson, hybr. nov. Fig. 1. (Putative parents: *Elymus sibiricus* L. × *Hordeum jubatum* L.)

Gramen perenne, caespitosum; culmi 40-85 cm alti 2-4 nodis; folia pilosa supra, scabra infra, 3-10 mm lata, 7-22 cm longa; spica arcuata, nutans, 6-15 cm longa; spiculae 3 ad nodum; spicula centralis 1-3 flosculis, sessilis; spiculae laterales 0-2 flosculis, subsessiles; flosculi steriles; glumae scabrae, aristiformes, usque ad 25 mm longae; lemmata scabra, 9-11 mm longa, aristis usque ad 25 mm longis; aristae curvantes ubi siccae; antherae 1.0-1.4 mm longae; $2n=28$.

HOLOTYPE: Roadside at junction of Fireweed Avenue and the Alaska railroad in Palmer, Alaska, 27 Jul 63, *Mitchell & Hodgson 980*, (ALA); isotypes (AES), (US), (ISC). Waste area at east end of east-west runway, Palmer, Alaska airfield, 23 Sep 64, *Mitchell & Hodgson 923A1*, paratype (AES). Experimental garden, Alaska Agricultural Experiment Station, Palmer, 4 Jul 67, *Mitchell 74D1*, *Mitchell 74D2*, paratypes (AES).

DISCUSSION.

An interesting pattern of intergeneric hybrid links has emerged from recorded crosses within the Triticeae of Alaska (Lepage 1952; Bowden 1958; Hodgson 1964; Hodgson and Mitchell 1965; Mitchell and Hodgson 1965) as illustrated in Figure 2. A number of reported crosses, that as yet have not been observed in Alaska, are also designated for species that are nevertheless represented in the state (Stebbins, et al. 1946a, 1946b; Lepage 1952, 1957; Bowden 1958, 1959). These are denoted by dashed lines in Figure 2. See Bowden (1967) for an excellent review of the intergeneric hybrids of the Triticeae of North America.

In the proposed reclassification of the taxa of Figure 2 (Löve and Löve 1965) *Elymus mollis* and *E. innovatus* Beal would be placed in *Leymus* and the wheat-grasses *Agropyron sericeum* Hitchc., *A. trachycaulum* (Link) Malte, and *A. violaceum* (Hornemann) Lange (= *A. latiglume* (Scribn. & Smith) Rydb.) combined with the wild ryes *Elymus sibiricus*, *E. glaucus* Buckley and *E. hirsutus* Presl.

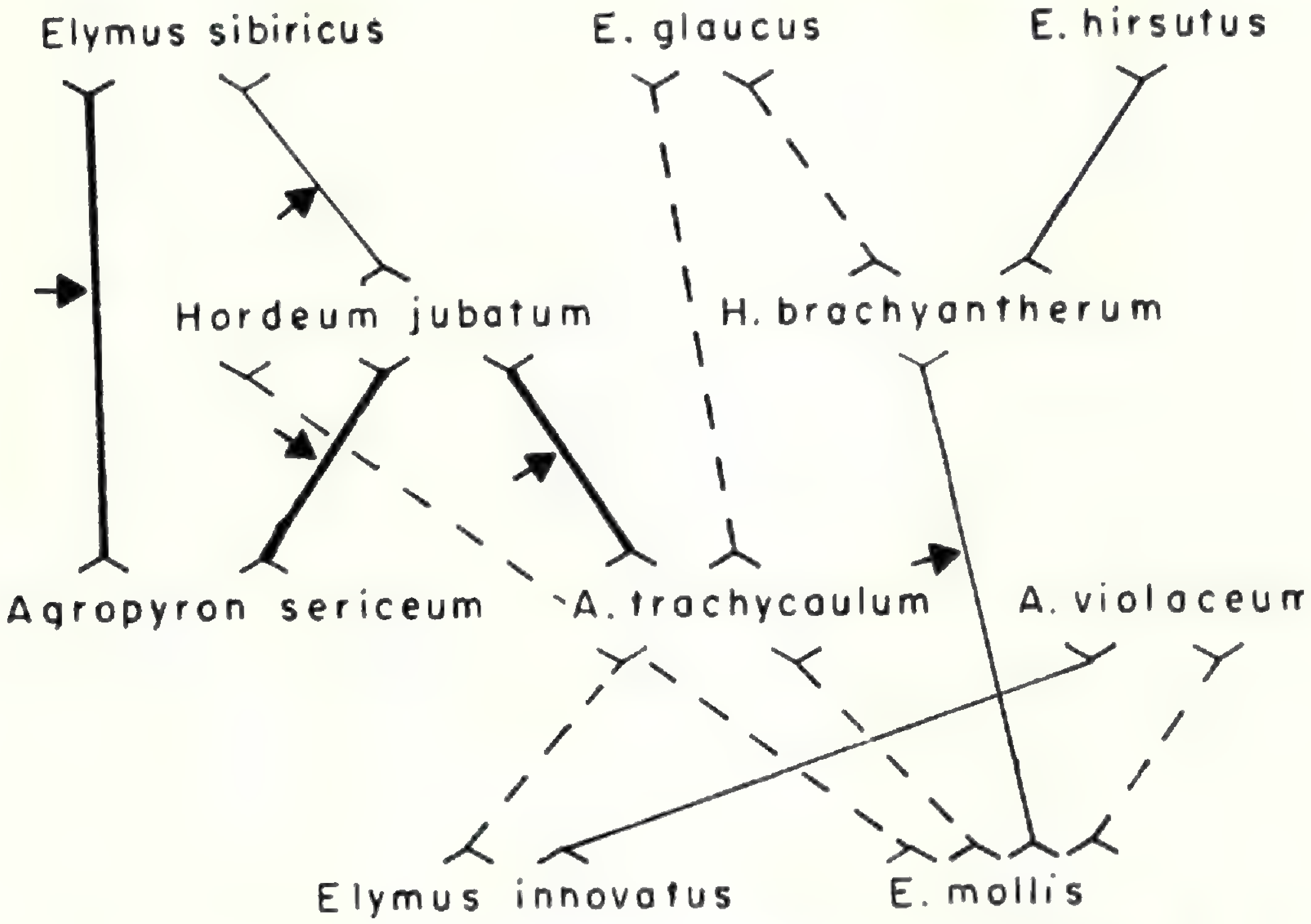

Fig. 2. Summary of intergeneric hybridization recorded for the Triticeae of Alaska. Heavy lines denote frequent occurrences, thin lines infrequent occurrences, and dashed lines recorded crosses not yet observed in Alaska. Five of the crosses, indicated by arrows, were observed in the vicinity of Palmer, Alaska.

under *Elymus*. Relationships expressed in Figure 2 indicate, however, an affinity between *Hordeum jubatum* and members of *Agropyron* which is as close as that between *Agropyron* and *Elymus*. Indeed, *Hordeum jubatum* and its close relative *H. brachyantherum*, which hybridize (Bowden 1962; Mitchell and Wilton 1964), serve as a hub relating all the taxa.

In none of the instances observed has the ability to cross appeared to have led to intergeneric introgression, this apparently being blocked by hybrid sterility. But the possibility of its occurring is not precluded, since colchicine treatment of × *Agroelymus palmerensis* Lepage (*Agropyron sericeum* × *Elymus sibiricus*) has demonstrated that fertility may be established in the allopolyploids. A wide array of recombinants has been produced through the C_3

generation from open pollination of fertile octoploids (Hodgson, unpublished data).

The incompleteness of the reproductive barriers between members of this generic complex, embracing as it does such morphologically disparate groups, seemingly confounds any attempt at a wholly satisfactory classification of the complex. Nevertheless, we consider it noteworthy that the character difference employed to discriminate *Agropyron* and *Elymus* is sufficiently strong to be reflected in crosses involving members of both genera with the same species, *Hordeum jubatum*. × *Agrohordeum* hybrids of this cross bear 1 to 2 spikelets at most nodes, rarely 3, while × *Elyhordeum* hybrids bear 3 well developed spikelets at a node.[1]

Acknowledgement. We thank Mrs. Zorka D. Mitchell for her assistance in composing the Latin description.

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GENERIC CONSIDERATIONS CONCERNING CARPHEPHORUS AND TRILISA (COMPOSITAE)

HENRY J.-C. HEBERT

The genus *Carphephorus* (Greek: karphe: chaff, and phoros: bearing) was established by Henri Cassini (1816). In describing this genus, Cassini stated that it differed from *Liatris* "par le clinanthe muni de grandes squamelles comme les calea, et par l'aigrette nonplumeuse" and consequently named the species *Carphephorus pseudoliatris;* in 1817, he placed *Carphephorus* near *Liatris*, in the natural tribe Eupatorieae.

In 1818, Cassini also erected the subgenus *Trilisa* which he elevated to generic rank in 1820 when he placed it with 15 other genera in the Eupatorieae. In establishing *Trilisa*, he stressed that it had the greatest affinity with *Carphephorus* from which it differed by the naked receptacle, but he was also careful to point out that *Trilisa odoratissima* "portoit accidentellement quelques squamelles". This last remark has been a central point of controversy over the generic limits of *Carphephorus* and *Trilisa*. No species were actually transferred to *Trilisa* until 1828, when Cassini cited *Liatris odoratissima* and *Liatris paniculata* of Willdenow (1803) as species of *Trilisa*. However, the genus *Trilisa* was not accepted at once, De Candolle (1836) and Torrey and Gray (1841) used it as a sectional name of the genus *Liatris*, but Bentham and Hooker (1873) referred to the incorrect use of Cassini's generic name for a section.

Carphephorus was thought to be of Siberian origin until Torrey and Gray (1841), prompted by a remark of Chapman, found that the chaffy receptacle had been overlooked by some botanists in describing other species and rightly recognized that *Carphephorus* referred to American plants. Consequently they proceeded to transfer *Liatris bellidifolia*, *Liatris tomentosa* and *Liatris corymbosa* to *Carphephorus*.

In 1924, the monotypic genus *Litrisa* (anagram of *Trilisa*) was described by Small for an endemic plant of Central

Florida. He concluded his description with the following remark: "Technically it is most closely related on the one hand to *Trilisa,* by its involucre, and on the other, to *Carphephorus,* by its chaffy receptacle." Apparently Small contradicted himself, because in his flora (page 1304, 1933) he keyed out *Litrisa* as having a naked receptacle. Robinson (1934) noticing the contradiction, examined the type as well as other material and apparently not finding any pales, he decided to transfer *Litrisa* to *Trilisa* rather than *Carphephorus,* implying as it had been customary, that *Trilisa* has no pales. So in addition to *T. odoratissima* and *T. paniculata,* a third species *carnosa* was added to the small genus *Trilisa.*

C. W. James (1958), upon examination of the three species of *Trilisa,* found that pales may be borne in any one of them and decided to merge at least *Trilisa carnosa* with the genus *Carphephorus,* using as primary generic distinction, the imbrication of the phyllaries. As the other two species had generally non-imbricate phyllaries, he considered that it was better "at the presnt time" to keep them in the segregate genus *Trilisa.*

The taxonomic discrepancies encountered in the *Carphephorus-Litrisa-Trilisa* complex cannot be attributed to thoughtless "splitting" or "lumping" but to incomplete information and inconsistent primary generic characters. Already in 1913, Robinson had noted in his studies of the Eupatorieae, that it is probable that "when these genera are more satisfactorily represented in herbaria some new and more convincingly natural re-adjustment of generic lines will become possible."

Bearing in mind that "fundamental" or "key" character can lead to misplacement of taxa, and that "every taxonomic character is potentially important" (Cronquist, 1957), a careful analysis of all available data was made. As the degree of relation may be determined by the "scientific" use of morphological similarity, a statistical evaluation of various characters that are "repeatable and verifiable" (Davidson,1963) was attempted to corroborate the results

obtained. The validity of this approach is based upon the premise that "similar or identical genetic systems operate to produce similar or identical phenotypes, always of course, allowing for the effects of the environment. If two plants have similar structures throughout, they are related." (Rollins, 1953)

The survey revealed a very close relationship between all seven species under consideration.

a) Karyotype: The cytological studies have yielded no evidence for the maintenance of the two species of *Trilisa* as distinct from *Carphephorus*. All seven species have 2n = 20. The karyotypes of *Trilisa odoratissima* and *Trilisa paniculata* have been found "to be indistinguishable from that of *Carphephorus*." (Gaiser, 1954). The seven species apparently have:

1 pair of long chromosomes with a median constriction
1 pair of long chromosomes with a submedian constriction
1 pair of long chromosomes with a subterminal constriction
3 pairs of chromosomes of median length with a median constriction
1 pair of chromosomes of median length with a submedian constriction
2 pairs of chromosomes of median length with a subterminal constriction
1 pair of short chromosomes with a median constriction.

These chromosomal similarities are particularly significant, because most of the other members of the Kuhniinae have chromosomes which differ either in shape and/or in number.

So far as known the species are perfectly distinctive, present relatively little variation and do not intergrade at all with others; interspecific hybridization has not been reported, in spite of overlapping ranges, similarities of habitats and coinciding flowering times. It is to be noted

that *Carphephorus* populations have generally a limited number of individuals and do not cover a wide area.

b) Distribution: The geographical distribution is a natural one; the seven species are confined to the southeastern coastal plain of the United States, generally on dry pine barrens.

c) Habit: All are perennial caulescent herbs with a nondeciduous rosette of basal leaves and alternate cauline leaves decreasing in size upwards. The blades are entire or shallowy toothed.

d) Basal leaves: Except for *Carphephorus pseudoliatris*, the basic pattern of the basal leaves is oblanceolate or spatulate. The ratio: maximal width of distal part/width of proximal part (measured at the quarter of the total length of the leaf) shows that the range of variation is approximately the same; only *C. pseudoliatris* and *C. carnosus* have less variation, the first having acicular leaves, the second, leaves tending to be linear-lanceolate. The ratio: maximal length/maximal width is not very significant due to the great variation of the length of the leaves.

e) Pubescence: The pubescence has been found to be of use as a character for specific differentiation between *C. tomentosus* and *C. bellidifolius* and between *T. paniculata* and *T. odoratissima*. The trichomes are generally nonglandular, multicellular, uniseriate, cylindrical, tapering towards the end and variable in length; in *T. paniculata*, the trichomes are biseriate.

The glandular trichomes are generally present in depressions below the epidermal surface and cause the characteristic punctation. These trichomes are biseriate in *C. carnosus* and *C. tomentosus*, and in the latter they are accompanied by laterally placed uniseriate filaments. They are uniseriate in the five other species (and occasionally also in *C. carnosus*) and usually occur singly, but in *C. pseudoliatris* and *C. corymbosus* they can also be found in groups of 2, 3 or 4. As noted by Gaiser (1954), a very reticulate pattern is evident in the distribution of the glandular trichomes.

f) Inflorescence: All species have the same basic cymose type of inflorescence, the heads being arranged in a corymbose fashion in six species, and in a racemose fashion in *T. paniculata*. The cymes are contracted in *C. pseudoliatris* and *C. carnosus*, and spreading in the other species.

g) Flowers: The number of flowers per head varies from 4 in *T. paniculata* to 46 in *C. pseudoliatris*. In the related genus *Liatris*, it varies from 3 to 70 (Gaiser, 1946). The floral parts are identical in all species. Their size varies but the range is not abnormal for a genus. The corolla for example, varies from 3.4 mm to 11 mm in this complex, while in *Liatris*, it varies from ca. 5 mm to ca. 20 mm (Gaiser, 1946). The corolla lobes show also a normal gradation in length, being longest in *C. bellidifolius* (Mean: 2.286 mm) and shortest in *C. carnosus* (Mean: 0.723). The anthers are definitely shorter in *C. carnosus*, *T. odoratissima* and *T. paniculata* than in the four other species. The apical end of the anthers is scarious in the seven species, but notched in only five of them: *C. pseudoliatris*, *C. tomentosus*, *C. bellidifolius*, *C. corymbosus* and *C. carnosus*.

h) Pappus: The bristles being of unequal length on each fruit, the overall length of the pappus was obtained by measuring the longest bristles. There is a variation from 3 to 10 mm, while in the genus *Liatris* it varies from 2.5 to 10 mm (Gaiser, 1946). The bristles generally number 30-55; in *T. odoratissima* they number 20-35.

i) Achenes: They are basically alike, being 10-ribbed, angular and narrowed towards the base. The mature achenes are of brown color, but in some cases they approach black. The length varies from 2 to 7 mm; in *Liatris* it varies from 3 to 10 mm (Gaiser, 1946).

j) Phyllaries and pales:

(1) Shape and size: The margin of phyllaries has proved to be a useful specific character; the margin can be pectinate-ciliate, erose-ciliate, eciliate or scarious; the apex also, varying from acute, mucronate to obtuse or rounded, is characteristic; on the other hand, characters like shape, width, length or pubescence vary much within

each species and can rarely be used as distinctive characters. It is to be noted that the pales generally resemble the inner phyllaries in shape, pubescence and size; occasionally, they are much narrower than the phyllaries.

(2) Number: The pales and the phyllaries which have been used as primary generic characters, show apparently a great range of numerical variation. But as the number of flowers per head varies much also, that range presents nothing unusual. For example, *C. pseudoliatris* which may have up to 46 flowers in one head has a mean number of pales of 23 and a mean number of phyllaries of 20; *T. paniculata* which often has only 4 flowers in one head has a corresponding low mean number of pales, 0.15 per head, and a mean number of phyllaries of 6.2 per head. It seems that the number of phyllaries and pales is related to the number of flowers. If one considers that the phyllaries and the pales are homologous — this is in accord with the theory of formation of the capitulum from an ancestral racemose umbel (Small, 1919) — a correlation can be seen between the number of phyllaries and pales (considered together) and the number of flowers. An increase in one set is matched by an increase in the other set; *T. paniculata* and *C. carnosus* which have the smallest number of flowers have also the smallest number of pales and phyllaries while *C. pseudoliatris* which has the greatest number of flowers has also the greatest number of pales and phyllaries. On the other hand, a statistical attempt to relate the number of flowers and either the number of pales or the number of phyllaries gave negative results, especially in the case of *C. pseudoliatris* which seems to possess too many pales and too few phyllaries. This stems from the difficulty of delimiting the pales and the phyllaries; in fact, no sharp line can be drawn between them, their position being often very indefinite and their shape identical. As a control, one species of *Liatris* has also been plotted and apparently does not contradict the theory that there is a correlation between flower-number and pale-phyllay-number. So, in the complex under consideration, it appears

sound to consider phyllaries and pales as a whole, because their structure is generally indistinguishable and seems to be controlled by the same genetic factor.

From these considerations, it is normal to expect fewer pales in a small head or even none, the flowers being almost all peripheral in position; thus, it would be an inadvisable decision to segregate *T. odoratissima* and *T. paniculata* simply because one fails to see pales in some heads. In the case of *T. odoratissima*, the pales were constantly seen in the plants I collected in September 1965, as well as in most herbarium specimens examined. Unfortunately no fresh material of *T. paniculata* could be examined and the herbarium specimens showed a great paucity of pales. However, James who had more opportunities of observing fresh material wrote in 1958: "Upon examination of all the species of the genera under consideration, I conclude that pales may be borne in any one of the species." As the pales are deciduous and tend to fall off when they are dry, it is possible that the "*odoratissima*" specimen examined by Cassini (1820) had lost most of its pales; that would have prompted Cassini to establish a distinction between *Carphephorus* and *Trilisa* and to write that "Les *Trilisa* ont la plus grande affinité avec le *Carphephorus*, qui n'en diffère que par le clinanthe squamellifère; et j'ai observé sur la *Trilisa odoratissima* que le clinanthe portoit accidentellement quelques squamelles." It is also possible that, finding only one or two pales in each head, or sometimes none, he concluded that the pales are not a permanent feature and occur only occasionally. At any rate, his word "accidentellement" is definitely too strong and conveys an erroneous idea about the presence of pales in *T. odoratissima*. Presumably, if Cassini had examined some fresh material, he would have merged *Trilisa* with *Carphephorus*, because he was not impressed by other differences. These considerations show how the exclusive use of the "presence of pales" is questionable as a primary generic criterion. As E. E. Sherff has pointed out: "There should not be separation of genera solely upon the presence or absence of one or

more supposedly diagnostic characters." (Reported by Turrill, 1942). This principle is particularly valuable in this case where the state of maturity of the plant can affect the character under consideration.

(3) Imbrication of phyllaries: The imbrication of phyllaries used by James to segregate "much more naturally" *Trilisa odoratissima* and *Trilisa paniculata* from *Carphephorus* is considered to be on a very weak basis (Shinners, 1946), especially when it is not supported by additional characters. Besides, it presupposes a sharp line where none can be drawn. In this complex, a gradation from 1 to 5 series of phyllaries is found. As the number of series is dependent on the number of phyllaries, it is evident that when the phyllaries number only 4 or 5 they can hardly overlap and be imbricated. So the imbrication of phyllaries is simply a qualitative factor based on quantitative data and cannot be taken as a distinctive character in itself. Upon examination of numerous specimens, I found that the number of series is highest in *C. tomentosus* and lowest in *T. paniculata.* But, for each species, the number varies and no line of demarcation can be set between them. Robinson (1934) had come to the same conclusion when he merged *Litrisa* with *Trilisa:* "The alleged involucral difference appears in fact a rather vague one of degree only."

Too much emphasis and exclusive reliance placed upon either the amount of pales or the arrangement of phyllaries has led to different results and varied segregation, but when the plants are considered as a whole and not as an aggregate of uncorrelated features, I find no solid ground to keep *Trilisa* as a separate genus. To maintain *Trilisa* distinct from *Carphephorus,* "because of tradition and inertia" (McVaugh, 1945) would impede a better understanding of their fundamental relationship and conserve an unwarranted segregation.

The generic transfer of *Trilisa* I propose is somewhat similar to the case of *Hymenopappus.* That genus had been placed in the tribe Helenieae, because the heads have no chaff; recent investigations showed that *Hymenopappus*

was not only more naturally placed in the Anthemideae, close to its obviously related prototype, the chaffy *Leucampyx,* but had to be united into a single genus, on the basis of the total data (Turner, 1956) ; since then the genus *Hymenopappus* includes "everything from perennial plants with chaffy receptacle and rayed heads to biennials with neither chaff nor rays." (Turner, 1956). With the transfer of both species of *Trilisa, Carphephorus* remains a homogeneous genus, much more than *Hymenopappus, Liatris* and many other composite genera. Only *T. paniculata* with its few pales, its rarely imbricate phyllaries and its cyme arranged in a paniculate fashion, would be slightly anomalous but would hardly alter the generic limits. Thus, if one compares the range of variation of the *Carphephorus-Trilisa* complex with the one of *Liatris,* one finds that there is no justification to keep *Trilisa* as a distinct genus. In fact, it is significant that *Liatris* which has been studied thoroughly by Robinson and Gaiser has not been split in spite of the numerous variations observed. There is no reason to consider *Carphephorus* a fundamentally different case. As pointed out by Blackwelder "group which cannot be distinguished at any particular level by the characters used for their neighbors must be combined at that level." (1963)

As I find that the biological status of all the species concerned may be best expressed by the grouping of all into one genus, I must follow the only alternative of uniting *Trilisa* to *Carphephorus.* This more comprehensive genus conforms to the definition of a genus given by Buxbaum (1951), as "the sum total of species belonging to a phylogenetic unit recognized as such by the unity of its morphological type." It is also in accord with Recommendation 3 of McVaugh (1945): "The most important criterion of any supposed genus is not the width of the gap between it and another, but its own biological unity. Homogeneity in many characters, regardless of the degree of overlapping of these characters with those of other genera, is the best indicator of this unity." No

doubt that those who like to make far too fine generic segregations will find that such a group is a return to the broad concept of genus in folk botany; these forget that "large genera may be quite as truly 'entities of nature' as small ones, . . . and from a practical and linguistic standpoint may be a far more useful concept." (Bartlett, 1940).

Carphephorus odoratissimus (J. F. Gmel) Hebert, comb. nov. based on *Chrysocoma odoratissima* J. F. Gmel, Syst. 2: 1204. 1792. Type: preserved in John Fraser's collection, in the British Museum, London. Place of origin: Carolina.

Carphephorus paniculatus (J. F. Gmel) Hebert, comb. nov. based on *Chrysocoma paniculata* J. M. Gmel, Syst. 2: 1204. 1792. Type: preserved in John Fraser's collection, in the British Museum, London. Place of origin: Carolina. Isotype: Lamarck Herbarium, Paris.

KEY TO THE SPECIES.

a) Heads with 12-43 flowers; pales 4-33 per head; phyllaries 12-33 per head; involucres 6-11 mm high.
  b) Basal leaves acerose, involute. .... 1. *C. pseudoliatris.*
  b) Basal leaves oblanceolate or spatulate, not involute.
    c) Phyllaries pubescent, their margins pectinate-ciliate. .... 2. *C. tomentosus.*
    c) Phyllaries glabrous or minutely hairy, their margins erose- or suberose-ciliate.
      d) Inflorescence an open slenderly-branched cyme; corolla lobes ca. 2-3 mm long. .... 3. *C. bellidifolius.*
      d) Inflorescence a dense compact corymbose cyme; corolla lobes ca. 1 mm long. .... 4. *C. corymbosus.*

a) Heads with 3-12 flowers; pales (0-) 1-3 per head; phyllaries 4-14 per head; involucres 3-6 mm high.
  e) Inner phyllaries pubescent, with pectinate-ciliate margins. .... 5. *C. carnosus.*
  e) Inner phyllaries glabrous, with eciliate margins.
    f) Stems glabrous; inflorescence an open and spreading corymbose cyme. .... 6. *C. odoratissimus.*
    f) Stems sparingly hirsute, viscid; inflorescence a thyrsoid panicle. .... 7. *C. paniculatus.*

BIOLOGY DEPARTMENT, SEYCHELLES COLLEGE,
SEYCHELLES ISLANDS.

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SPIRANTHES OVALIS. NEW FOR KANSAS

While collecting in an oak-hickory woodland 2 miles north and ¾ mile east of Baldwin City, Douglas County, Kansas, a specimen of *Spiranthes ovalis* Lindl. was taken on October 13, 1967 *(Johnson 1184,* KANU*)*. The plant was associated with *Botrychium dissectum* Spreng. var. *obliquum* (Muhl.) Clute, *Corallorhiza odontorhiza* (Willd.) Nutt., and *Monotropa uniflora* L. This orchid has previously been reported from Florida to Texas, north to Virginia Kentucky, Indiana, and Missouri. In Missouri the species is known only from Mississippi, St. Louis, and Jackson Counties. My collection is an extension westward of the range of the species.

KERMIT L. JOHNSON
UNIVERSITY OF KANSAS, LAWRENCE, *66044*.

AN EXAMPLE OF A VERNONIA HYBRID IN A DISTURBED HABITAT

Samuel B. Jones, Jr.

The identification of ironweeds has been a persistent source of difficulty, resulting in large part from the blurring of species lines by hybridization. Cain (1944) suggested that hybridization in *Vernonia* increased with the arrival of European man who cut timber, built roads, drained land, and created numerous ecological niches not previously present. He presented the hypothesis that *Vernonia* × *illinoensis* Gleas. was derived from hybridization and introgression of three species, *V. missurica* Raf., *V. fasciculata* Michx and *V. altissima* Nutt., and this hybridization was augmented by the disturbance of the habitat by man. A relationship between natural hybridization and disturbed habitats has been recognized for some time. Anderson's classic paper (1948) summarizes our present day concept of the habitat and its significance in natural hybridization. Anderson points out that hybrids often survive where man has disturbed or "hybridized" the habitat. Hybrid swarms are most often found in disturbed habitats, particularly those which are intermediate between the habitats of the parents and to which neither parent is as well adapted as are the hybrids.

In 1963, I found an interesting example of *Vernonia* in a disturbed habitat near Leakesville in Greene County, Mississippi. In the area concerned, *Vernonia altissima* grows along the edge of the wet, bottomland forest near the Chickasawhay River with many of the plants of the population growing in standing water. This population of *V. altissima* is not pure but apparently contains genes of *V. missurica* reflecting the introgression mentioned above. This does not, however, have any bearing on the problem at hand and to avoid confusion I will call this taxon *V. altissima*. Southeast of the river is a high, very dry, sandy turkey oak and longleaf pine ridge with *V. angustifolia*

abundant. Some years ago, a road with a long fill was constructed from the wet bottomland to the dry ridge (Fig. 1) and a hybrid swarm of several hundred clones representing both F_1 and backcross types can now be found on this fill. The ironweeds of this swarm are intermediate in morphological features and habitat requirements between the narrow leaved *V. angustifolia* and the wide leaved *V. altissima.* The roadfill evidently provides a number of ecological niches between the contrasting wet and dry sites resulting in a typical example of a "hybridized" habitat.

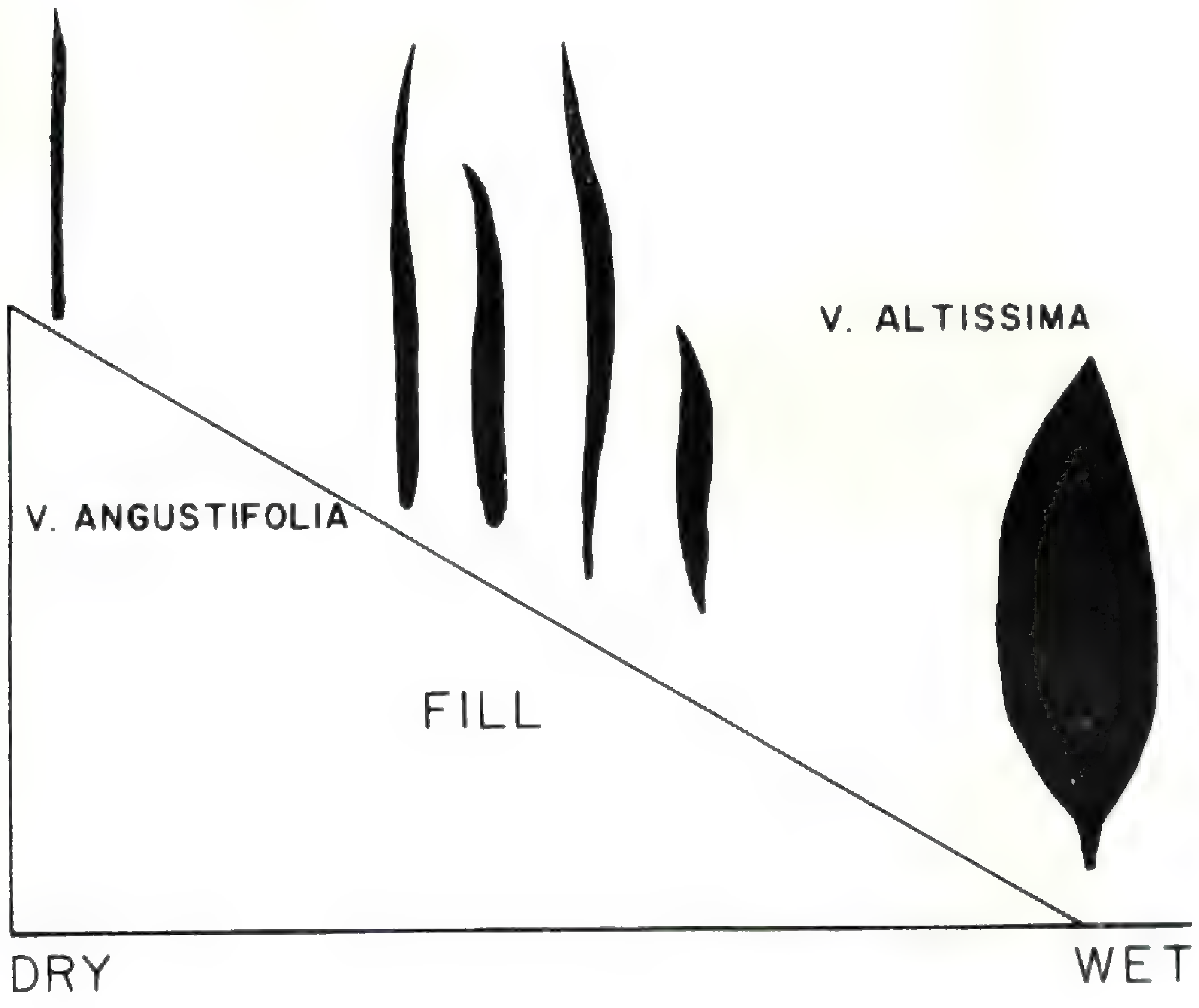

Fig. 1. Diagrammatic scheme of the habitats and leaf tracings of the parents and hybrids.

To assess the degree of interbreeding, local population samples of about 25 specimens each were collected from the two extreme habitats and along the roadfill in 1963, 1964, and 1966. In addition, individuals of the present species and selected hybrids were transplanted to the

experimental garden and greenhouse. That natural hybridization could be the cause of the intermediates was demonstrated by crossing *Vernonia altissima* and *V. angustifolia*. The artificial F_1 hybrids appeared to be vigorous and similar to the hybrids found on the fill. Backcrosses were also made between the field collected hybrids and the two parental species. Pollen stainability tests with anilin blue in lacto-phenol indicated that there was no appreciable difference in stainability between the two parental species, the natural hybrids, the backcross types, or the artificial F_1 hybrids. The average stainability ranged from 87 to 99 percent. The local population samples were measured and scored; the important morphological features are compared in Table 1. A scatter diagram is presented in Figure 2.

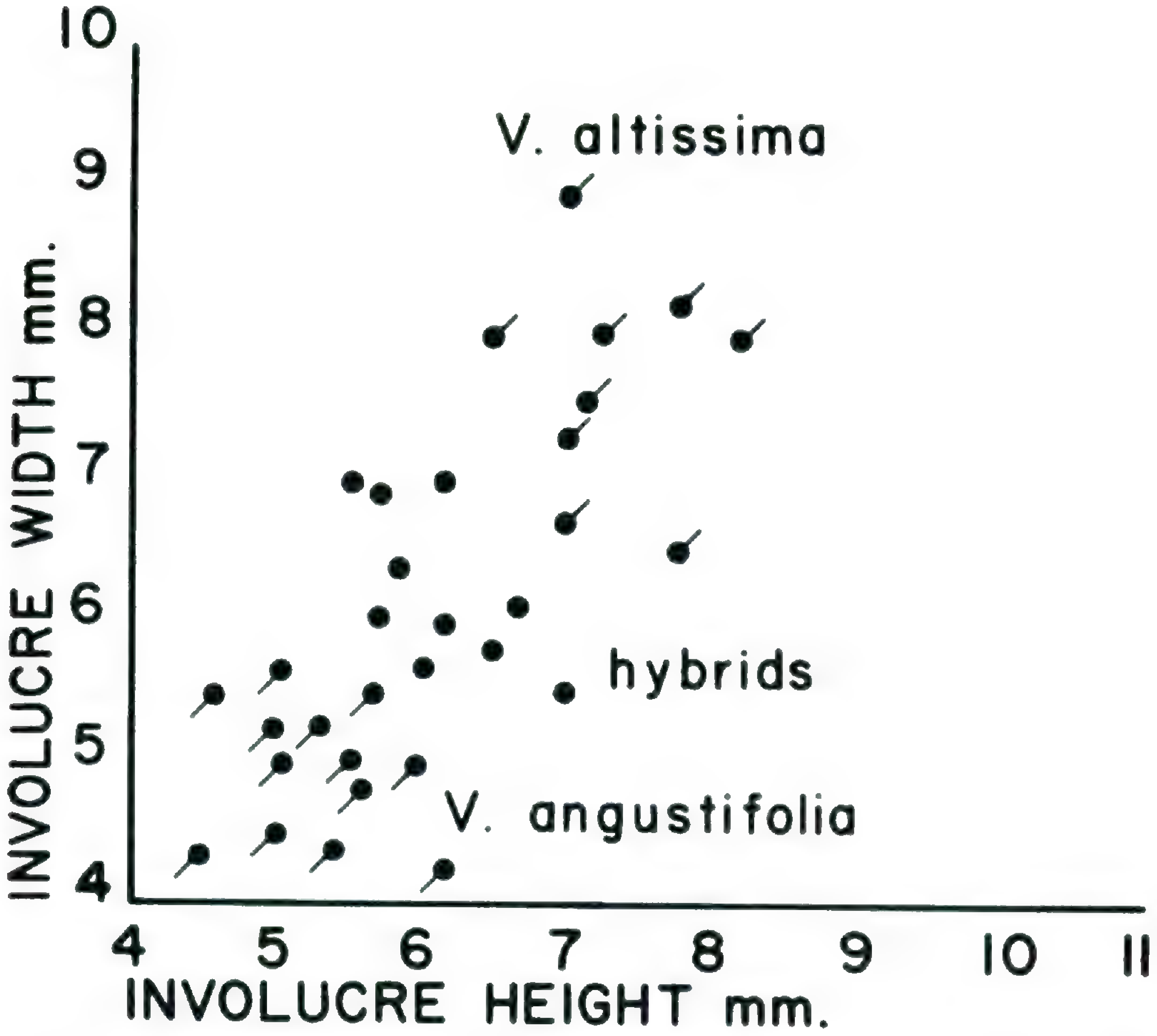

Fig. 2. Scatter diagram of *Vernonia altissima*, *V. angustifolia*, and their hybrids from local population sample.

TABLE 1. Comparison of certain morphological features of *Vernonia angustifolia*, *V. altissima* and their natural hybrids[a]

Characteristic	*V. angustifolia*	Hybrids	*V. altissima*
Leaf Shape	linear	narrowly lanceolate	elliptic to elliptic-lanceolate
Leaf Surface (lower)	scabrous	scabrous to sparsely tomentose	sparsely short tomentose
Leaf Margins	callus teeth	remotely toothed	teeth present
Leaf Length	46 — 98 mm	75 — 137 mm	103 — 158 mm
Width	1.0 — 2.4 mm	3.7 — 10.6 mm	21 — 31 mm
Flowers/head	10 — 16	16 — 22	25 — 40
Involucre Width	4.2 — 6.0 mm	4.8 — 8.0 mm	6.1 — 9.0 mm
Involucre Height	4.7 — 6.2 mm	6.7 — 8.2 mm	5.5 — 7.8 mm
Involucre Shape	narrowly campanulate	campanulate	broadly campanulate
Bract Tips	acute to acuminate	mucronate to acute	mucronate

[a]Based on studies of local population samples, see text.

Pollen size was determined by staining mature pollen grains with anilin blue in lacto-phenol and measuring them with an eyepiece micrometer. The sizes of the pollen grains are given in Table 2. The pollen grains of the hybrids were intermediate in size between those of the parents and had a greater standard deviation than those of the parents. Both taxa have a chromosome number of n = 17.

TABLE 2. Diameter of the pollen grains[a]

Taxon	$\bar{X}$	Range	s
V. angustifolia	38.8	37.4 — 40.8	1.24
Hybrids	41.2	39.1 — 44.2	2.51
V. altissima	43.0	40.8 — 44.2	1.53

[a] n = 125, from 5 plants of each taxon; measurements in microns.

The ranges of *Vernonia altissima* and *V. angustifolia* are partially sympatric. They are, however, usually ecologically isolated. The former grows in moist or even wet areas at the edge of low woods or in open fields, while the latter is found in well drained upland habitats such as scrub oak sand hills or dry longleaf pine woods. Studies based on the Greene County, Mississippi site clearly indicate that ecological isolation is not always effective and that the hybrids are intermediate between their parents in both morphological characteristics and in their habitat requirements. Introgression between *V. altissima* and *V. angustifolia* is certainly conceivable and may serve to enlarge the ecological parameters of those two taxa. I have observed this natural hybridization in scattered locations in both Alabama and Mississippi where the ranges of these two taxa are sympatric. At other sites, however, only one or two hybrids were noted. This is probably due to the lack of suitable ecological niches for the hybrids. Since hybridization has ben observed at other locations, it is possible that introgression is occurring where the species are sympatric.

DEPARTMENT OF BOTANY,
UNIVERSITY OF GEORGIA, ATHENS 30601

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WOLFFIA IN NEW HAMPSHIRE. Two small additions to the flora of New Hampshire were discovered on 8 October 1967 when I stopped to investigate an unusual greenish coloration in the shallow water of a small roadside pond. I had visited this pond about a year previously but found no noteworthy plants there at that time. To my surprise I now discovered, growing in great profusion, two of our most diminutive flowering plants:

WOLFFIA COLUMBIANA Karsten. Profusely abundant. Forming, with *Wolffia punctata* Griseb. and *Lemna minor* L., a dense floating layer about the margins of a small pond near Cohas Brook; on the east side of Interstate Highway 93 approximately 2 miles north of the Manchester City Boundary. Manchester, Hillsborough County, New Hampshire. 8 October 1967, *Countryman 1718*.

WOLFFIA PUNCTATA Grisebach. Data as above except less abundant. *Countryman 1719*.

The pond was revisited on 4 November 1967 in company with Albion R. Hodgdon. The *Wolffia* was still plentiful at that date. We were able to collect nearly pure samples of both species of *Wolffia* by pouring a pail of the pond water through two graduated sieves (kitchen tea strainers). The coarser sieve held back *Lemna minor* and miscellaneous debris while the finer sieve was of such a size as to contain the *Wolffia*. In the samples so collected about 95% of the material was *W. columbiana*, the balance *W. punctata*.

Specimens of both species have been preserved in FAA in sealed glass ampoules (see Dore, W. G., *Canadian Field Naturalist* 1957, 71: 10-16) and deposited in the herbaria of the New England Botanical Club and the University of New Hampshire.

WM. D. COUNTRYMAN
NORWICH UNIVERSITY, NORTHFIELD, VERMONT 05663

LEGUMINOSAE OF MEXICO — FABOIDEAE

I. SOPHOREAE AND PODALYRIEAE

VELVA E. RUDD

INTRODUCTION

The Leguminosae, or Fabaceae, is one of the largest and most important families of flowering plants. In Mexico, where corn and beans, tortillas and frijoles, have long been staples of diet, the legume family probably ranks second only after the grass family in importance to the basic economy.

Of a worldwide total of about 600 genera of Leguminosae, slightly over 100 are native to Mexico. Approximately another 20 to 30 genera have been introduced, many of which have been naturalized. The figures are somewhat larger if one recognizes the many segregate genera such as have been ascribed to *Acacia*, *Pithecellobium*, and *Astragalus*.

The leguminous genera known to occur in Mexico include not only beans but other edible seeds, fruits, and vegetative parts utilized as food for man and animals. Many trees provide economic products such as lumber, resins, and pharmaceuticals; some are cultivated as ornamentals.

Early reports of the natural history of Mexico mention leguminous plants utilized by the Indians, especially for medicinal purposes. Oviedo[1], writing in 1526, mentioned that many kinds of beans, "fesoles", were gathered in great abundance, especially in "Nueva España é Nicaragua", some with yellow seeds, others spotted, "pintados de pecas." The Badianus manuscript, an Aztec herbal of 1552[2], includes colored illustrations of several legumes appearing to be species of *Calliandra*, *Mimosa*, *Haematoxylon*, and *Phaseolus*. White incense, possibly from *Myroxylon*, is mentioned in the text. Hernandez' report on the plants of

[1]Fernández de Oviedo y Valdéz, Gonzalo. História general y natural de las Indias. Madrid, 1851-1855.

[2]Cruz, Martín de la, and Juan Badianus. English translation by Emily Walcott Emmart. The Badianus manuscript — an Aztec herbal. 1940.

Mexico, written in 1570-1575[3], includes a great many legumes, some clearly recognizable, others dubiously so. From an illustration, as well as the text, "hoitziloxitl", the "bálsamo de indias", is without doubt identifiable as *Myroxylon.*

Taxonomic works, such as those of Linnaeus, Willdenow, Miller, Kunth, DeCandolle, and Bentham, included descriptions of new Mexican Leguminosae based on early collections, especially those of Houstoun, Humboldt and Bonpland, Sessé and Mociño. They will be cited in the following taxonomic text.

In 1880 Hemsley[4] listed the legumes of Mexico and Central America as completely as then known from the herbarium material at Kew. Unfortunately, although collections were cited, descriptions were given only for new species; and there are no keys. The woody species of legumes were included in Standley's Trees and Shrubs of Mexico[5], but this treatment is long out of date. There never has been a complete treatment of the herbaceous species.

For the "North American Flora" the Mimosoideae, as Mimosaceae[6], and the Caesalpinioideae, as Caesalpiniaceae[7], were revised by Britton and Rose, and the Faboideae, as Fabaceae[8], were presented, in part, by various authors, chiefly Rydberg.

Perusal of Langman's tremendous bibliography[9] will indicate how much has been published on the Mexican flora and vegetation. Nevertheless, there is no adequate treat-

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[3]Hernández, Francisco. Spanish translation by José Rojo Navarro. História de las plantas de Nueva España. Mexico, 1942-1946.

[4]Hemsley, W. B. in Godman and Salvin. Biologia Centrali-americana. Botany 1: 225-364. 1880.

[5]Standley, P. C. Trees and Shrubs of Mexico. Contributions from the U. S. National Herbarium 23: 348-515. 1922; appendix 1657-1667. 1926.

[6]Britton, N. L. and J. N. Rose. North American Flora 23: 1-194. 1928.

[7]Britton, N. L. and J. N. Rose. North American Flora 23: 201-349. 1930.

[8]Rydberg, P. A. North American Flora 24: 1-462. 1919-1929.

[9]Langman, I. K. A selected guide to the literature on the flowering plants of Mexico. 1964.

ment for general determination of Mexican legumes, especially the faboid genera.

In the preparation of this synopsis of the Leguminosae of Mexico, many general works have been consulted, including the Genera Plantarum of Bentham and Hooker[10], Taubert's treatment of the Leguminosae for Die Natürlichen Pflanzenfamilien[11] and the supplement by Harms[12], The Genera of Flowering Plants by Hutchinson[13], and the Index Nominum Genericorum[14]. For economic uses, the works of Martínez, Las Plantas Medicinales de México[15] and Plantas Utiles de la Flora Mexicana[16], and Timbers of the New World by Record and Hess[17] have been important sources of information. Burkart's Las Leguminosas Argentinas[18] has been especially valuable. Also helpful have been such floristic works as the Flora of Yucatan by Standley[19], the Flora of Guatemala by Standley and Steyermark[20], Legumes of Texas by Turner[21], Arizona Flora by Kearney and Peebles[22], and the Vegetation and Flora of the Sonoran Desert, by Shreve and Wiggins[23].

[10]Bentham, G. and J. D. Hooker. Genera Plantarum 1: 434-600. 1865.

[11]Taubert, P. in Engler and Prantl. Die Natürlichen Pflanzenfamilien III, 3: 70-388. 1891-1894.

[12]Harms, H. in Engler and Prantl. Die Natürlichen Pflanzenfamilien III, 3. Nachträge 2: 30-34, 190-203. 1900.

[13]Hutchinson, J. The genera of flowering plants 1: 221-489. 1964.

[14]Index Nominum Genericorum. International Association for Plant Taxonomy. Utrecht. 1954 —

[15]Martínez, M. Las plantas medicinales de México, ed. 4. 1959.

[16]Martínez, M. Plantas útiles de la flora mexicana. 1959.

[17]Record, S. J. and R. W. Hess. Timbers of the New World. 1943.

[18]Burkart, A. Las leguminosas argentinas, ed. 2. 1952.

[19]Standley, P. C. Flora of Yucatan. Field Museum of Natural History, botanical series 3: 157-492. 1930.

[20]Standley, P. C. and J. A. Steyermark. Flora of Guatemala. Fieldiana: Botany 24(5): 1-368. 1946.

[21]Turner, B. L. The legumes of Texas. 1959.

[22]Kearney, T. H. and R. H. Peebles. Arizona flora, 395-484. 1960.

[23]Shreve, F. and I. L. Wiggins. Vegetation and flora of the Sonoran desert 1: 585-731. 1964.

As indicated in the key, I am treating the Leguminosae as one large family subdivided into three subfamilies, the Mimosoideae, the Caesalpinioideae, and the Faboideae, the latter also known as the Papilionoideae and the Lotoideae. In this study the Faboideae will be presented first for more or less arbitrary reasons, principally, because this subfamily was only partly treated in "The North American Flora" mentioned above.

My interpretation is generally conservative, with the genera arranged in the Dalla Torre and Harms[24] sequence, and ten tribes, essentially as delimited by Bentham, and followed by Taubert and others. I believe that Hutchinson's separation of the "Fabaceae" into 50 tribes is unduly divisive. Perhaps, a system somewhat intermediate between Bentham's and Hutchinson's can be developed, but, for purposes of an introductory key to tribes in this paper, the former will be followed.

At the suggestion of the late Dr. Faustino Miranda I am attempting to provide fairly full descriptions, synonymy, and citations of material studied. To avoid unnecessary bulk, however, I am excluding citations of Old World synonymy unless pertinent to Mexican taxa. Relevant monographic works will be cited under the genera, but the authors' interpretations will not necessarily be followed.

This work is based chiefly on herbarium material, as indicated by the citations. The abbreviations of herbarium names are those of Lanjouw and Stafleu[25]. I am grateful to the curators of those many institutions for making their specimens available to me.

The citations of "F.M.Neg." refer to Field Museum negatives of a series of photographs taken in European herbaria by J. F. Macbride during 1929 to 1939.

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[24]Dalla Torre, C. G. and H. Harms. Genera siphonogamarum. 1900-1907.

[25]Lanjouw, J. and F. A. Stafleu. Index herbariorum I. The herbaria of the world, ed. 5. 1964.

SYSTEMATIC TREATMENT

Leguminosae: Legume or bean family

Leguminosae Juss. Gen. 345. 1789, nom. cons. TYPE: *Faba* Mill. (= *Vicia* L. p.p.)

Fabaceae Lindl. Nat. Syst. ed. 2, 148. 1836, nom. alt. TYPE: *Faba* Mill. (= *Vicia* L. p.p.)

Trees, shrubs, or herbs, the stems sometimes twining; leaves commonly alternate, rarely opposite, compound, sometimes simple, usually stipulate, sometimes stipellate; flowers commonly bisexual, 5-merous, solitary or in compound inflorescences, axillary or terminal; sepals free or united, 4 or 5, rarely 1, then spathaceous; petals free or united, 5, sometimes fewer or lacking; stamens commonly 5-∞, sometimes reduced to only 1 fertile member, the sterile members may be present or sometimes reduced to staminodes, the filaments free or united, the anthers 2-celled, dehiscing lengthwise or by terminal pores; pistil usually 1, the ovary superior, 1-locular, 1-∞ ovulate; fruit a legume, dehiscent or indehiscent, 1-many-seeded, 2-valved, but may be modified as a drupe, samara, follicle, or loment; seed commonly with a coriaceous testa, reniform, lenticular, or spherical, sometimes alate, sometimes arillate, the hilum orbicular to linear, sometimes circumcinct, the endosperm little or none.

Distribution: Worldwide.

KEY TO SUBFAMILIES OF LEGUMINOSAE

Flowers actinomorphic, radiate and regular; corolla and calyx valvate in bud (except calyx imbricate in Parkieae); stamens 4-∞; leaves commonly bipinnate, sometimes pinnate or reduced to phyllodes .... Mimosoideae

Flowers generally zygomorphic, sometimes subactinomorphic; corolla and calyx imbricate in bud or, sometimes, valvate.

- Uppermost (adaxial) petal enveloped by the other petals in bud; stamens (fertile) 1-∞, commonly 10 or fewer; leaves usually pinnate, sometimes bipinnate, rarely simple .... Caesalpinioideae
- Uppermost (adaxial) petal exterior in bud, enveloping the other petals; stamens 10, rarely fewer; leaves simple or pinnate, never bipinnate .... Faboideae

Leguminosae subfamily FABOIDEAE

Leguminosae subfam. Faboideae.[26] TYPE: *Faba* Mill. (= *Vicia* L. p.p.)

Papilionaceae Giseke, Praelect. Ord. Nat. Pl. 415. 1792.

Fabaceae H. G. L. Reichenbach, Consp. Regni Veg. 149. 1828.

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[26]The use of "Faboideae," based on Fabaceae, agrees with article 19 of the International Code of Botanical Nomenclature, 1966.

Leguminosae fam. *Papilionatae* A. Braun in Ascherson, Fl. Prov. Brandenb. Einleitung 67. 1864.

Leguminosae subfam. *Papilionoideae* Robinson & Fernald, Gray's New Man. Bot. ed. 7, 500. 1908.

Papilionaceae subfam. *Lotoideae* Luerssen, Grundzüge Bot. 379. 1877. Type: *Lotus* L.

Leguminosae subfam. *Lotoideae* (Luerssen) Rehder, Journ. Arn. Arb. **26**: 477. 1945.

Characters those of the family except as noted in the key to subfamilies, viz., leaves never bipinnate; flowers with adaxial petal exterior in the bud, enveloping the other petals, if present; stamens commonly 10, rarely fewer.

The taxa not typified above presumably were based on *Faba* Mill.

KEY TO TRIBES OF SUBFAMILY FABOIDEAE IN MEXICO

a. Flowers with stamens distinct, the filaments separate to the base. *b.*
- *b.* Leaves pinnately 5- many-foliolate. .... 1. SOPHOREAE
- *b.* Leaves digitately 1-3-foliolate. .... 2. PODALYRIEAE

a. Flowers with stamens united, all or most of the filaments joined, at least in part, monadelphous or diadelphous. *c.*
- *c.* Legumes commonly indehiscent, drupes, samaras, or loments, sometimes compressed, nonalate, usually more than 1 cm. long. *d.*
  - *d.* Fruits articulated, the joints usually separating at maturity; stamens monadelphous or diadelphous 5:5 or 9:1. .... 7. HEDYSAREAE
  - *d.* Fruits mostly drupaceous or samaroid, sometimes compressed, nonalate; stamens commonly monadelphous, the vexillar filament sometimes separating from the others .... 8. DALBERGIEAE
- *c.* Legumes 2-valved, usually dehiscent or, if indehiscent, small, but a few mm. long. *e.*
  - *e.* Leaves digitate. *f.*
    - *f.* Leaflets serrate or denticulate; leaves commonly 3-foliolate, rarely more or less; stamens diadelphous 9:1. .. 4. TRIFOLIEAE
    - *f.* Leaflets entire; leaves 1-many-foliolate; stamens monadelphous or diadelphous. *g.*
      - *g.* Stamens monadelphous, the filaments uniform in width, forming a closed tube or open sheath, the anthers dimorphic, alternately basifixed and dorsifixed. .... 3. GENISTEAE
      - *g.* Stamens diadelphous, the vexillar stamen free, the others united, alternate filaments commonly broadened at the apex, the anthers uniform. .... 5. LOTEAE
  - *e.* Leaves pinnate. *h.*
    - *h.* Leaf rachis terminating in a tendril or bristle; leaves even-pinnate; stamens 9, monadelphous, or 10, diadelphous 9:1. .. .. 9. VICIEAE

h. Leaf rachis usually with a terminal leaflet, without tendrils or bristles; leaves mostly odd-pinnate; stamens mostly diadelphous 9:1, sometimes pseudomonadelphous with the vexillar filaments partially adherent to the adjacent filaments (Galegeae). *i*.

i. Leaflets serrate or denticulate. .... 4. TRIFOLIEAE

i. Leaflets entire or sometimes dentate or lobate (Phaseoleae). *j*.

j. Flowers in umbels, loosely capitate, or solitary in the axils; stamens with filaments commonly broadened at the apex; anthers uniform. .... 5. LOTEAE

j. Flowers in racemes, panicles, or spikes; stamens with filaments essentially uniform in width; anthers uniform or sometimes dimorphic. *k*.

k. Leaves commonly with 5 or more leaflets, estipellate. .... 6. GALEGEAE

k. Leaves commonly 3-foliolate or sometimes with 1, 5, or 7 leaflets, usually stipellate. .... 10. PHASEOLEAE

Tribe 1. SOPHOREAE

Sophoreae Spreng. Anleit. 2, 2: 741. 1818. Type: *Sophora* L.

Trees, shrubs, or herbs, sometimes climbing; leaves pinnately 1-many-foliolate; stipules present or absent; stipels rarely present; inflorescences racemose or paniculate; flowers with the corolla zygomorphic or subactinomorphic; calyx valvate or imbricate in bud; petals free or with the keel petals joined; stamens 10 or fewer, the filaments separate to the base, equal or alternately subequal in length, the anthers essentially uniform, dorsifixed, oblong to ellipsoid; ovary 1-many-ovulate, the style glabrous, at least toward the apex; fruit 2-valved, dehiscent or indehiscent, sometimes samaroid; seed with hilum apical, lateral, or, rarely, circumcinct.

KEY TO MEXICAN GENERA OF SOPHOREAE

a. Leaflets with resinous, pellucid lines and dots; fruit elongate-samaroid, 1-seeded at apex. *b*.

b. Anthers oblong, about 4-4.5 mm. long; leaves 7-11-foliolate; leaflets mostly ovate, acute, or acuminate; ovary glabrous. .... 2. MYROXYLON

b. Anthers elliptic, about 1 mm. long; leaves 11-23-foliolate; leaflets mostly oblong, obtuse; ovary pubescent, at least at the base. .... 3. MYROSPERMUM

a. Leaflets lacking pellucid lines but sometimes with minute punctae; fruit 1-15-seeded, not elongate-samaroid as above. *c*.

c. Fruit about 5 mm. thick or less, the valves thinly coriaceous, usually somewhat marginate or alate; flowers not papilionaceous. *d*.

d. Flowers with 5 subequal petals; ovary with filiform style, the stigma minutely capitate-penicillate; fruit about 5-9 cm. long. .... 1. SWEETIA

d. Flowers with 1 petal; ovary with sessile, peltate stigma; fruit semiorbicular, about 4 cm. long or less. .... 4. ATELEIA

c. Fruit about 5-20 mm. thick, the valves coriaceous or lignous, not alate; flowers papilionaceous with 5 petals. *e.*

e. Standard petal pubescent on the outer face; fruit orange- or fulvo-velutinous, usually brownish when dry, the valves enrolled after dehiscence; seeds elliptic or cylindrical, red, darkening when dry, the hilum subapical; leaflets with tertiary veins scalariform; lateral leaflets alternate to subopposite. .... 5. DUSSIA

e. Standard petal glabrous on the outer face; fruit glabrous or pubescent, the valves not distorted after dehiscence; seeds subglobose, the hilum apical; leaflets with tertiary veins mostly reticulate, the lateral leaflets essentially opposite. *f.*

f. Flowers with curved style, the stigma bilobed, lateral; fruit compressed, somewhat constricted between the seeds but not moniliform; seeds red or bicolored red and black. .... 6. ORMOSIA

f. Flowers with style essentially straight, the stigma minutely capitate-penicillate, terminal; fruit terete or nearly so, torulose or moniliform; seeds red, brownish, or yellowish. .... 7. SOPHORA

1. SWEETIA Spreng.

Sweetia Spreng. in L. Syst. Veg. **2**: 171, 213. 1825, nom. conserv., non DC. 1825. TYPE: *S. fruticosa* Spreng. Brazil.

Acosmium Schott in Spreng. in L. Syst. Veg. **4**, Append.: 406. 1827. TYPE: *A. lentiscifolium* Schott in Spreng. Brazil.

Leptolobium Vog. Linnaea 11: 388. [Feb.] 1837, non Benth. [June] 1837, 1838. Lectotype: *L. dasycarpa* Vog. (Mohlenbrock, Webbia **17**: 233. 1963). Brazil.

Thalesia Mart. ex Pfeiffer, Nom. 2(2): 1384. 1874, nom. nud. based on *Leptolobium* Vog.; non Raf. 1818, nom. nud.

Reference: R. H. Mohlenbrock, Webbia **17**: 223-263. 1963.

Trees, unarmed; leaves alternate, imparipinnate, commonly 5-21-foliolate, the leaflets alternate; stipules and stipels minute or lacking; inflorescences axillary or terminal, racemose or paniculate; flowers small; calyx turbinate-campanulate with 5 subequal lobes, valvate or subimbricate in bud; corolla with 5 free, subequal, whitish petals; stamens 10, rarely 5, the filaments free, subequal, the anthers uniform, ellipsoid, dorsifixed; stigma terminal; fruit indehiscent com-

pressed 1-4-seeded; seeds brown or reddish brown, elliptic to ovate, compressed, the hilum apical, elliptic.

About 20 species, chiefly in South America.

1. **Sweetia panamensis** Benth. Jour. Linn. Soc. Bot. 8: 263. 1865. TYPE: *S. Hays 267*, Panamá [Canal Zone]. Figure 1.
Dalbergia laevigata Standl. Trop. Woods 12: 5. 1927. TYPE: *S. J. Record s.n.*, British Honduras.

Tree, to about 40 m. tall; leaves 5-15-foliolate, the axis about 8-20 cm. long, puberulent or subglabrous, the lateral leaflets alternate, the blades coriaceous or subcoriaceous, ovate to ovate-oblong, about 2-9.5 cm. long, 1-4 cm. broad, the apex obtuse or acute, retuse, the base rounded, the upper surface nitid, glabrous, the lower surface moderately pubescent, glabrate, the secondary venation inconspicuous, the tertiary venation reticulate, the terminal leaflet sometimes larger than the laterals; inflorescences with axes moderately pubescent, the bracts and bracteoles linear, 1-3 mm. long; flowers about 6 mm. long, fragrant; calyx moderately pubescent to subglabrous, 3-4 mm. long, the lobes and tube about equal in length; corolla white or cream-colored, the petals glabrous, subequal, spatulate, emarginate, clawed; stamens 10, with the filaments about as long as the petals or slightly longer, the anthers less than 1 mm. long; ovary sparsely pubescent to glabrous, the style glabrous or subglabrous, the stigma terminal, minutely capitate-penicillate; fruit indehiscent, coriaceous, light brown or stramineous, glabrous at maturity, reticulate, compressed, 1-3-seeded, oblong or elliptic, the ends acute to obtuse, about 5-9 cm. long, (1.5-) 2-2.5 cm. broad, about 5 mm. thick at the seeds, otherwise less than 1 mm. thick; seeds lustrous, subovate, about 8 mm. long, 6 mm. broad, and 2-3 mm. thick, the hilum about 1 mm. long.

Distribution: In moist forest up to about 800 meters elevation, southern México to northern Colombia and northwestern Venezuela.

MEXICO: VERACRUZ: Campo Experimental de Hule, El Palmar, Zongolica, *Vera-Santos 3264* (MICH). Minatitlan, *Saenz s.n.* (MICH). Near Cordoba, *Froehling s.n.* (MICH).

GUERRERO: La Parota, *Langlassé 383* (GH, K, MEXU, P, US). Agua de Correa, Jimalcota, *Langlassé 685* (GH, K, P, US).

OAXACA: Tuxtepec, *Miranda 4153* (MEXU, US); *Gómez-Pompa 1264* (MEXU); *Sousa 251* (MEXU). Tuxtepec, El Naranjal, *Miranda 4297* (MEXU, US). Tuxtepec, Chiltepec, *Martínez-Calderón 62* (GH, MEXU, UC, US), *564* (MEXU, UC, US). Santa María de Chimalapa, *Mell s.n.* (US). "Matilde, Valle Usmacín," *Reko 4095* (US). Ubero, *Ll. Wil-*

liams 9165 (DS, F, P, UC) [same collection? but locality as Fortuño, Veracruz (A)].

CHIAPAS: Cacaluta, Escuintla, *Matuda 16587* (MEXU), *16663*

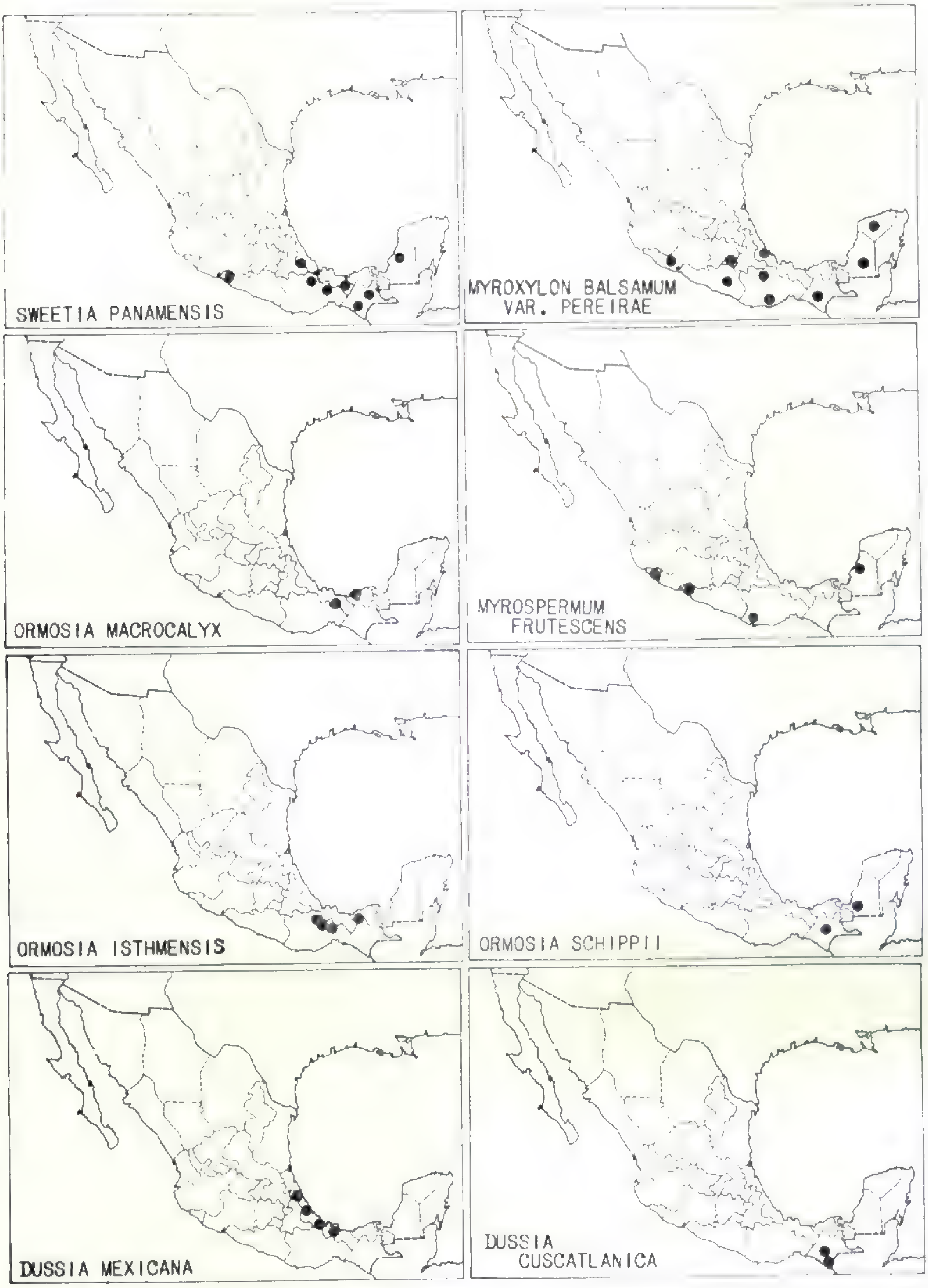

Fig. 1. Geographic distribution of *Sweetia, Myroxylon, Myrospermum, Ormosia,* and *Dussia* in Mexico.

(MEXU), *16984* (MEXU). La Arena, Palenque, *Enríquez s.n.* [*Miranda 7604*] (MEXU, US). "Estación Lacandon a Tabasco Hacienda, Palenque, *Miranda 7285* (MEXU).

CAMPECHE: Champotón, *Miranda 8046* (MEXU, US).

Local names: Chacté, chakté, chile, palo chile, huasillo, huesillo, huesito (México); guayacán (México, Costa Rica); chichipate (Guatemala, El Salvador, Honduras); quina silvestre (Guatemala); Billy Webb (British Honduras); carboncillo (Costa Rica); malvecino (Panamá); rejo (Colombia); vera de agua (Venezuela).

The wood of this species is strong and durable. The timber is used for heavy construction such as bridges, for wagons and carts, and for various implements.

2. MYROXYLON L. f.

Myroxylon L. f., Suppl. 34, 233. 1781, nom. conserv., non J. R. et G. Forster, 1776. TYPE: *M. peruiferum* L. f. Colombia.

Toluifera L. Sp. Pl. 384. 1753. TYPE: *T. balsamum* L. Colombia.

Myrospermum sect. *Myroxylon* (L. f.) DC. Prodr. **2**: 95. 1825.

Reference: H. Harms, Notzbl. Bot. Gart. Berlin **5**: 85-98. 1908.

Trees, unarmed; leaves alternate, imparipinnate, 5-15-foliolate; leaflets alternate, with pellucid lines and dots; stipules and stipels minute or lacking; inflorescences axillary or terminal, racemose; flowers small; calyx turbinate-campanulate with 5 subequal lobes, valvate in bud; corolla with 5 free petals, subequal except for a broader standard; stamens 10, the filaments free, essentially equal, the anthers uniform, oblong, acuminate, sagittate, dorsifixed; fruit indehiscent, samaroid, commonly with 1 apical seed; seeds subreniform, resinous, the hilum elliptic, subapical.

Two or three species, in Mexico, Central and South America, sometimes cultivated.

1. **Myroxylon balsamum** (L.) Harms, Notzbl. Bot. Gart. Berlin **5**: 94. **Figure 1.**

Tree, to about 40 m. high; bark gray, resiniferous; leaves 5-11-foliolate, the axis about 6-15 cm. long, puberulent to subglabrous, the lateral leaflets alternate, the blades moderately coriaceous, with pellucid lines and dots, predominantly ovate, sometimes elliptic, 3-14 cm. long, 1-7 cm. broad, the apex obtuse to acuminate, sometimes retuse, the base rounded to subcordate, the surfaces essentially glabrous at maturity, the upper surface nitid or subnitid, the secondary venation relatively inconspicuous; inflorescences with axes puberulent,

the bracts and bracteoles deltoid, the bracts 1-3 mm. long, the bracteoles about 1 mm. long; flowers 12-15 mm. long; calyx minutely pubescent, suffarinose, 5-8 mm. long, the lobes about 1 mm. long, the tube 4-7 mm. long; corolla white, the petals glabrous, spatulate, clawed, subequal except the standard 2-3 times as broad as the others; stamens 10, the filaments essentially equal in length, slightly longer than the calyx, the anthers oblong, resinous, acuminate, sagittate, about 4-4.5 mm. long; ovary and style glabrous, the stigma terminal, truncate; fruit indehiscent, coriaceous, light brown or stramineous, glabrous, samaroid with 1 or, rarely, 2 apical seeds, essentially straight or curved, 6-11 cm. long exclusive of stipe 5-15 mm. long, 2-3 cm. broad and 1 cm. thick at the seed, the basal portion sterile, alate, compressed, 4-7 cm. long, 1-3 cm. broad, 1 mm. thick or less; seed reniform, light brown, resinous, about 15-20 mm. long and 5-8 mm. in diameter.

1a. **Myroxylon balsamum** (L.) Harms, var. **balsamum.**

Toluifera balsamum L. Sp. Pl. 384. 1753. TYPE: Specimen not known; Tolú, near Cartagena, Colombia.

Myroxylum toluiferum A. Richard, Ann. Sc. Nat. Paris **2**: 171, 172. [June] 1824, nom. nov. based on *Toluifera balsamum* L.

Myroxylon toluifera H.B.K. Nov. Gen. **6**: 375. [August] 1824, nom. nov. based on *Toluifera balsamum* L.

Myrospermum toluiferum (A. Rich.) DC. Prodr. **2**: 95. 1825.

The typical variety is characterized by relatively large fruit, 8-11 cm. long, straight or somewhat curved, 2-3 cm. broad with the margins approximately parallel. The leaflets are glabrous, acuminate or sometimes acute at the apex.

Distribution: In forest, up to about 300 meters elevation, Panamá, Colombia, and Venezuela; perhaps elsewhere.

Local names: Bálsamo, balsam of Tolú, Tolú balsam (general); cereipo, estoraque, roble maría, olor, tache (Venezuela); uscum (Bolivia).

The most important difference between the varieties seems to be in the physical and chemical properties of the balsam. The typical variety is mentioned above because it is possible that it occurs in Mexico, particularly in Yucatan. However, because many of the herbarium vouchers are sterile and information concerning the balsam is unavailable, I am citing all Mexican collections as var. *pereirae*.

1b. **Myroxylon balsamum** var. **pereirae** (Royle) Harms, Notizbl. Bot. Gart. Berlin **5**: 95. 1908. Figure 1.

Myrospermum Pereirae Royle, Man. Mat. Med. ed. 2, 414. 1853. TYPE: *Jonathan Pereira s.n.*, El Salvador.

Myrospermum Sonsonatense Pereira [as Pareira] ex Oerst. Vid. Medd. Nat. For. Kjbenh. **27**. 1855, based on "Myrospermum of Sonsonate" of Pereira, Pharm. Journ. **10**: 280. 1851.

Myroxylon Pereirae (Royle) Klotzsch, Bonplandia **5**: 275. 1857.

Toluifera Pereirae (Royle) Baill. Hist. Pl. **2**: 383. 1870.

Myroxylon sonsonatense [Oerst.] auct. ex Flückiger & Hanbury, Pharmacogr. 179. 1874.

Toluifera balsamum L. var. *β Pereirae* (Royle) Baill. Traité de bot. méd. 676. 1883.

The fruit of this variety tends to be smaller than that of the typical variety, 6-8 cm. long, straight or, sometimes, strongly curved, the winged lower portion usually narrower toward the stipe. The leaflets commonly are smaller than average for the species, glabrous or with a trace of pubescence along the midvein, the apex acute or, less commonly, breviacuminate.

Distribution: In moist or dry forest at elevations up to about 1000 meters, southern Mexico to Panamá (and Colombia?). Introduced elsewhere.

MEXICO: Without exact locality, *Sessé & Mociño 1039* (F, MA), [Pavon Herb. No. 856] (G).

VERACRUZ: "Mataluca near Cordova", *Finck s.n.* (K, BM). "Km. 10 carretera Cosolapa a El Palmar, a la izquierda de Pueblo Nuevo", *Chavelas, Péres, & Sarukhán 24* (US); *Chavelas* ES-1693 (US).

MORELOS: Cuernavaca, *Mell 1* (NY). Oaxtepec, *Reko s.n.* (MEXU, MICH); *Miranda 4106* (MEXU); *Palacios s.n.* (MICH); *Rzedowski 19450* (US). Soconusco, *Altimirano 276* (MEXU).

MICHOACÁN: Coalcoman, Trojes, *Hinton 12296* (K, NY, US), *12298* (K, MICH, NY, US). Coalcoman, Villa Victoria, *Hinton 12540* (K, US), *13901* (NY, US). Hacienda Coahuayula, *Emrick 29* (F).

GUERRERO: Montes de Oca, Jalapa, *Urbina s.n.* (MEXU).

OAXACA: Pochutla, Cafetal Calverio, *Conzatti, Reko & Makrìnius 3079* (US). Cuicatlán, El Faro, *Conzatti 3820* (MEXU). Cerro Espino, *Reko 3622* (MEXU).

CHIAPAS: Without exact locality, *Becerra 54* (MEXU). Cacaluta, Escuintla, *Matuda 16529* (F, NY, MEXU, MICH), *16554* (F, MEXU, MICH, NY). Piedra Rojada, *Enriquez* [Miranda No.] *6740* (MEXU).

CAMPECHE: Campo Experimental Forestal Tropical "El Tormento", Km. 5, carretera Escárcega a Candelaria, *Hernández X. & Chavelas ES-291* (US). "Km. 30 carr. Escárcega-Chetumal", *Chavelas*

& *Gómez-Pompa ES-762* (US). "Km. 30, Escárcega-Silvituc, *Gómez-Pompa 1327* (MEXU, US).
YUCATAN: Without exact locality, *Gaumer s.n.* (A, POM, US), *716* (US), *776* (BM, F). Merida, *Schott 804* (BM, F, US).

Local names: Bálsamo, bálsamo del Perú, arbol del bálsamo, balsamito, bálsamo de San Salvador, bálsamo negro, cedro chino, chuchupate, chucté, hoitziloxitl [Nahuatl], naba [Maya], nabal, palo del bálsamo, palo de trapiche, semillas del obispo, yagaguienite (Mexico); chirraca (Costa Rica); olor, tache (Colombia).

The balsam, or resin, is used as incense and in medicinal preparations. The wood is suitable for fine cabinet work. The trees are sometimes planted as shade for coffee plantations.

3. MYROSPERMUM Jacq.

Myrospermum Jacq. Enum. Pl. Carib. 4, 20. 1760. TYPE: *M. frutescens* Jacq. Colombia.
Myrospermum Sect. *Calusia* Bert. ex DC. Prodr. **2**: 94. 1825.
Calusia Bert. ex. Steud. Nom. ed. 2, **1**: 262. 1840, nomen in synon.

Reference: F. Klotzsch, Bonplandia **5**: 272-277. 1857.

Trees or shrubs, unarmed; leaves alternate, imparipinnate; leaflets alternate, with pellucid dots and dashes; stipules and stipels minute or lacking; inflorescences axillary or terminal, racemose; flowers fairly small; calyx turbinate-campanulate with 5 subequal lobes, valvate in bud; corolla with 5 free petals, subequal except for a broader standard; stamens 10, the filaments free, essentially equal, the anthers uniform, ellipsoid, dorsifixed; fruit indehiscent, samaroid, commonly with 1 apical seed; seed reniform, the hilum elliptic, subapical.

One or two species, from southern Mexico to northern South America.

1. **Myrospermum frutescens** Jacq. Enum. Pl. Carib. 4, 20. 1760. TYPE: *N. J. Jacquin s.n.*, Colombia. Figure 1.

Bannisteria purpurea Mill. Gard. Dict. ed. 8. 1768, in part, non L. 1753. TYPE: *W. Houstoun s.n.*, "Campechy," Mexico.
Myroxylon frutescens (Jacq.) Willd. Sp. Pl. **2**: 546. 1799.
Myrospermum emarginatum [Bert. ex Klotzsch] Klotzsch, Bonplandia **5**: 277. 1857. TYPE: *C. G. Bertero s.n.* [Balbis Herb no. *3165*]. Colombia.

Calusia (as *Caluria*) *emarginata* Bertero ex Klotzsch, Bonplandia 5: 277. 1857. nomen in synon.

Tree or shrub, to about 5 m. high; leaves about 10-23-foliolate, the axis 8-17 cm. long, puberulent or glabrous; leaflets oblong to elliptic, 1-5 cm. long, 0.5-2 cm. broad, the apex obtuse to emarginate, the base rounded, the surfaces usually glabrous, sometimes puberulent, the lower surface sometimes glaucous, the secondary venation inconspicuous; bracts and bracteoles deltoid, 1-2 mm. long, 1 mm. wide, or less; flowers about 12-17 mm. long, fragrant; calyx argenteo-velutinous to subglabrous, 5-6 mm. long, the lobes about 1 mm. long or less; petals white, sometimes with pink, purplish, or yellow markings, pubescent at the apex, otherwise glabrous, spatulate, clawed, the standard about twice as broad as the wing and keel petals; ovary pubescent, at least at the base, 5-7-ovulate (fide Klotzsch), the style glabrous, the stigma terminal, subcapitate, minutely penicillate; fruit 4-5 (-6.5) cm. long including stipe about 5 mm. long, 12-15 mm. wide at widest part of wing, the fertile, terminal portion about 15 mm. long and 10 mm. wide; seed about 8 mm. long, 3 mm. wide, and 2 mm. thick.

Distribution: Deciduous woods, southern and western México to northern South America.

MEXICO: COLIMA: Near Río Salado, *Miranda 9053* (MEXU); *McVaugh & Koelz 1441* (MICH).

GUERRERO: Cutzamala, Coyuca, *Hinton 7291* (F, GH, K, US).

OAXACA: Near Tehuantepec, *Alexander 111* (F, GH, NY, US), *168* (NY).

CHIAPAS: Rancha La Lanza, near Tiltepec, west of Tonalá, *Miranda 7268* (MEXU, US).

Campeche: "Campechy," *Houstoun s.n.* (BM).

Local names: Cuerillo, guachipilin hediondo (Mexico); arco, laurel macho (Costa Rica); balsamito, mano de pilón (Colombia).

The plants are balsamiferous but less so than those of *Myroxylon.*

4. ATELEIA (DC.) Benth.

4. Ateleia (DC.) Benth. Comm. Leg. Gen. 37. 1837 (preprint); Ann. Wien. Mus. Naturg. 2: 101. 1838. TYPE: *Pterocarpus ateleia* DC. Mexico.

Pterocarpus section *Ateleia* DC. Prodr. 2: 419. 1825; Mem. Leg. 393. 1826.

Ateleia [Sessé & Mociño ex] DC. Prodr. **2**: 419. 1825; Mem. Leg. 394. 1826, nomen in synon.

References: R. H. Mohlenbrock, Webbia **17**: 153-186. 1962; V. E. Rudd, Contr. U. S. Nat. Herb. **32**: 385-411. 1968.

Shrubs or trees; leaves alternate, imparipinnate; leaflets alternate or subopposite; stipules apparently lacking or reduced to a tuft of hairs; stipels lacking; inflorescences racemose, sometimes paniculate, axillary or terminal, about 5-20 cm. long with about 10 to several hundred flowers; bracts small, deltoid or linear, sometimes persistent, sometimes caducous; bracteoles apparently lacking; flowers 5-14 mm. long; calyx regular, cyathiform, valvate or subimbricate in bud, truncate or subtruncate with 5 lobes or teeth about 0.5 mm. long or less; petal 1, white or yellowish, clawed, cucullate, sometimes expanded, spatulate at anthesis, glabrous or pubescent on the outer face, the margin erose or sinuate; stamens 6-10 (-11), sometimes varying in number in different flowers of the same inflorescence, the filaments alternately subequal in length, shorter than the petal, the anthers uniform, ellipsoid, 1 mm. long or less, dorsifixed; ovary 1-2-ovulate, the stigma essentially sessile, peltate, obliquely terminal; fruit indehiscent, samaroid, semiorbicular with a narrow wing along the upper suture, 2-valved, commonly 1-seeded, compressed, stipitate; seeds reddish-brown to dark brown, reniform, the hilum lateral, orbicular or elliptic.

KEY TO SPECIES OF ATELEIA

a. Leaflets with lower surface moderately to densely pubescent with crispate or spreading hairs, sometimes glabrescent. *b.*

b. Fruit, including stipe, 3.5-4 cm. long. *c.*

c. Flowers 10-14 mm. long, the calyx 4-6.5 mm. long, the petal pubescent; fruit pubescent, usually glabrescent, the wing along the upper suture very little developed; seed 9-15 mm. long (México; Michoacán). .... 1. *A. arsenii*

c. Flowers less than 10 mm. long, the calyx 2-3 mm. long, the petal glabrous; fruit glabrous with the wing along the upper suture 1-2.5 mm. wide. *d.*

d. Leaflets mostly rounded at the base, asymmetrical; petiolules 3-4 mm. long; fruit 1.5-1.8 cm. wide, including wing 2-2.5 mm. wide (Michoacán). .... 3. *A. truncata*

d. Leaflets mostly cuneate at the base, essentially symmetrical; petiolules 2 mm. long or less; fruit 1-1.5 cm. wide including wing 1-2 mm. wide (Campeche). .... 8. *A. gummifera*

b. Fruit, including stipe, less than 3.5 cm. long. *e.*

e. Leaflets mostly rounded at the base, asymmetrical. *f.*

f. Fruit tomentose (Chiapas). .... 6. *A. tomentosa*

f. Fruit essentially glabrous, the stipe sometimes puberulent. *g.*

g. Leaflets moderately pubescent below; fruit 2.5-3 cm. long, including stipe, and about 1.5 cm. wide (Nayarit; western Jalisco). .... 4. *A. standleyana*

g. Leaflets tomentulose below; fruit 2-2.3 cm. long, including stipe, and 1-1.2 cm. wide (Veracruz; Oaxaca; Chiapas). .... 5. *A. pterocarpa*

e. Leaflets mostly cuneate at base, essentially symmetrical (Campeche) .... 8. *A. gummifera*

a. Leaflets with lower surface glabrous or moderately pubescent with appressed or subappressed hairs. *h*.

h. Fruit 3-4 cm. long, including stipe, and 1.5-2 cm. broad including wing 2-3 mm. wide; leaflets rounded, asymmetrical at base (Nayarit: Isla María Madre). .... 2. *A. insularis*

h. Fruit 2-3.5 cm. long, including stipe, and 1-1.5 cm. broad including wing 1-2 mm. wide; leaflets cuneate to obtuse, essentially symmetrical at base. *i*.

i. Leaflets predominantly ovate, almost as wide as long, the petiolules 2-3 mm. long (Chiapas). .... 7. *A. albolutescens*

i. Leaflets predominantly oblong, about twice as long as wide, the petiolules 2 mm. long or less (Campeche). .... 8. *A. gummifera*

1. **Ateleia arsenii** Standl. Contr. U.S. Nat. Herb. **20**: 174. 1919. TYPE: *Bro. G. Arsène 6655*, México. Figure 2.

Shrub, to about 1 m. tall; leaves 13-23-foliolate, the axis tomentulose, glabrescent, about 10-20 cm. long; leaflets with blades ovate, ovate-oblong, elliptic, or lanceolate-ovate, 1-5.5 cm. long, 0.5-2.5 cm. broad, acute to obtuse, the base obtuse, usually oblique, the upper surface moderately crisp-pubescent, glabrescent, the lower surface moderately crisp-pubescent, the secondary veins moderately conspicuous, the petiolules about 1 mm. long or less, crisp-pubescent; bracts deltoid to linear, 1-3 mm. long; flowers 10-14 mm. long; calyx tomentulose, 4-6.5 mm. long; petal 10-14 mm. long, 6-8 mm. broad, pubescent on the outer face, usually expanded at anthesis; ovary villous; fruit crisp-pubescent, glabrescent, 3.5-4 cm. long and 1.2-1.8 cm. broad, the upper margin essentially straight or slightly convex, incompletely developed, 1 mm. wide or less, the stipe 1-1.5 cm. long; seed 9-15 mm. long, 6-7 mm. wide, and about 2 mm. thick, the hilum about 0.8 mm. in diameter.

Distribution: In oak woods, at elevations of about 1800 to 3000 meters. Known only from México and Michoacán.

MEXICO: MÉXICO: Nanchititla, *Hinton 3421* (A, F, G, K, MEXU), *6158* (A, F, K, MICH, US), *7621* (A, F, G, K); *Matuda 37472* (MEXU). Temascaltepec, *Hinton 407* (BM), *3526* (F, K), *4240* (A, BM, F, G, K), *5286* (A, BM, F, G, K, NY, US), *6093* (A, BM, G, K, MEXU, NY, US).

MICHOACÁN: Quinceo, vicinity of Morelia, *Arsène 2790* (GH, L, NY fragment, US). "Morelia, flanca du Quinceo, *2500*? ou *3200*? fruits en 1910," *Arsène 6655* (NY fragment, US TYPE).

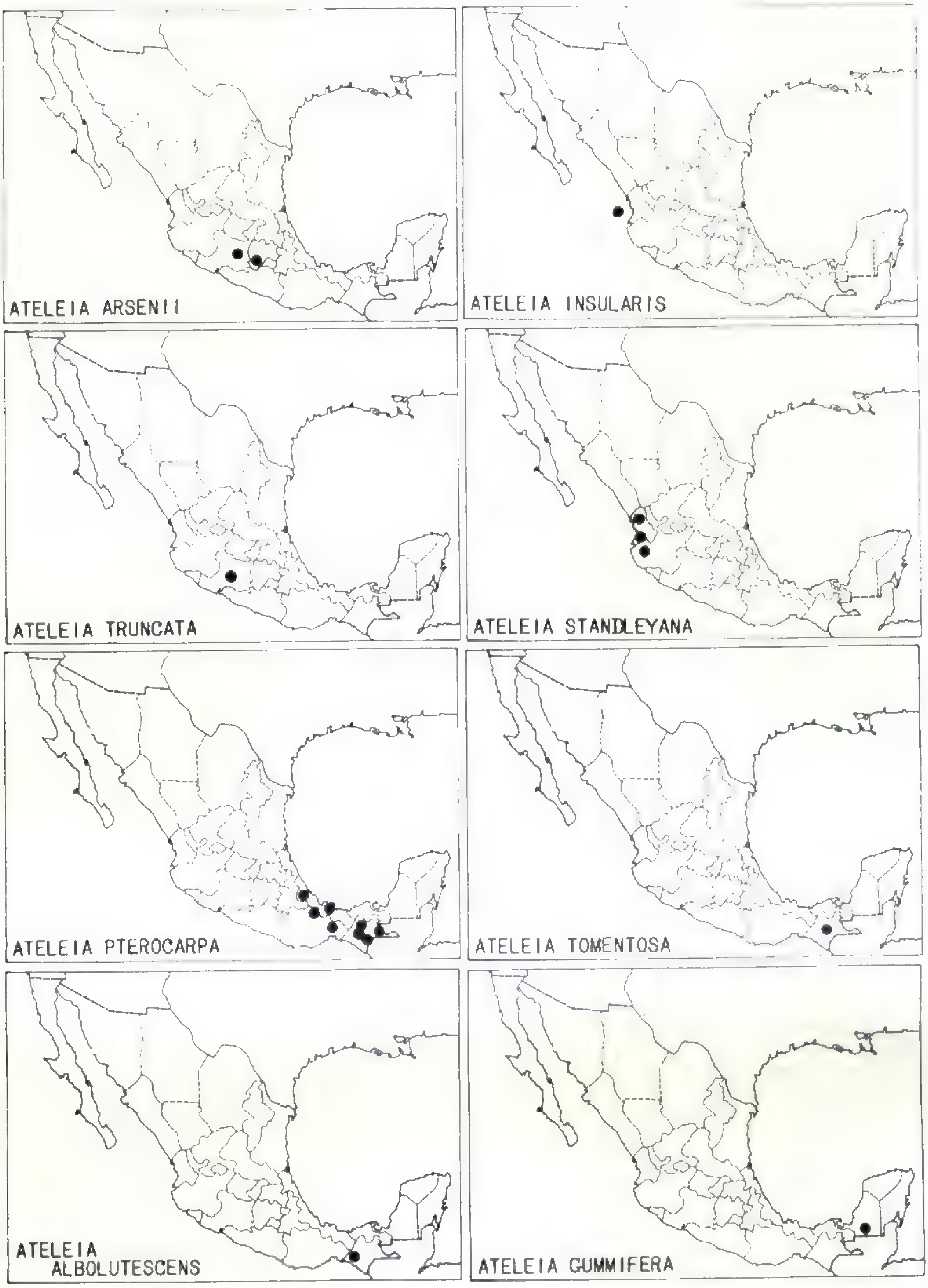

Fig. 2. Geographic distribution of *Ateleia* in Mexico.

Local name: Haba de venado (Temascaltepec, México). According to Hinton (no. 3421) this species provides food for deer.

2. **Ateleia insularis** Standl. Contr. U.S. Nat. Herb. **20**: 175. 1919. TYPE: *E. W. Nelson 4186*, México. Figure 2.

Tree or shrub, to about 5 m. tall; leaves 9-15-foliolate, the axis puberulous with appressed or subappressed hairs, glabrescent; leaflets with blades ovate, 2-6.5 cm. long, 1-3.5 cm. broad, obtuse, the base obtuse, oblique, the surfaces glabrous except for a few appressed or subappressed hairs, especially along the midvein, the secondary veins moderately conspicuous, the petiolules 2-4 mm. long, puberulent, glabrescent; bracts deltoid, 0.5 mm. long or less; flowers 6-7 mm. long; calyx puberulent, 2.5-3 mm. long; petal 6-7 mm. long and about 4 mm. broad, glabrous, usually expanded at anthesis; ovary essentially glabrous; fruit glabrous, 3-4 cm. long, 1.5-2 cm. broad, the upper margin convex with a wing 2-3 mm. wide, the stipe 0.8-1 cm. long; seed about 7 mm. long, 4 mm. wide, and 4 mm. thick, the hilum about 0.8 mm. in diameter.

Distribution: Known only from Isla María Madre, at elevations of 700 meters or less.

MEXICO: NAYARIT: Isla María Madre, *Nelson 4186* (A, F, NY fragment, P, US TYPE); *Ferris 5573* (A, DS, US), *5742* (DS, US); *Howell 10471* (A); *Maltby 73* (US); *Mason 1843* (K, US).

Essentially the only difference separating this species from *A. standleyana* and *A. truncata* is the presence of appressed rather than crispate or patent pubescence.

3. **Ateleia truncata** Mohlenbrock, Webbia **17**: 180, fig. 4, 17. 1962. TYPE: *F. Salazar s.n.*, México. Figure 2.

Tree or shrub; 11-13-foliolate, the axis about 9-10 cm. long or more, tomentulose; leaflets with blades elliptic to ovate or obovate, 4-6 cm. long and 1.5-3 cm. broad, obtuse, retuse, the base cuneate to obtuse, oblique, the upper surface crisp-pubescent, glabrescent, the lower surface moderately pubescent, the hairs crispate or somewhat spreading, the secondary veins moderately conspicuous, the petiolules 3-4 mm. long, tomentulose; bracts deltoid, 0.5-1 mm. long; flowers 6-7 mm. long; calyx tomentulose, glabrescent, 2.5-3 mm. long; petal about 6-7 mm. long, 4 mm. wide, glabrous, probably expanded at anthesis (mature flowers not seen); ovary glabrous; fruit glabrous, 3.5-4 cm. long, 1.5-1.8 cm. broad, the upper margin convex with a wing 2-2.5 mm. wide, the stipe about 1 cm. long; seed (submature) about 7 mm.

long, 4 mm. broad, and 2 mm. thick, the hilum about 1 mm. in diameter.

Distribution: Known only from the type collection.

MEXICO: MICHOACAN: Hacienda de la Huerta, near Apatzingán, *Salazar s.n.* March 6, 1914 (MEXU, US TYPE).

Local name: Piojillo.

The species is characterized by the relatively large, glabrous fruit.

4. **Ateleia standleyana** Mohlenbrock, Webbia 1: 179, fig. 4, 16. 1962. TYPE: *J. N. Rose, P. C. Standley, & P. G. Russell 14474*, México. Figure 2.

Tree, to about 12 m. tall; leaves 9-15-foliolate, the axis about 12-20 cm. long, velutinous, glabrescent; leaflets with blades ovate to suborbicular, 1-8.5 cm. long, 1-5.5 cm. broad, obtuse to acute, the base obtuse, oblique, the upper surface minutely crisp-pubescent to subappressed-pubescent along the midvein, otherwise glabrous, the lower surface moderately crisp-pubescent, glabrescent, sometimes glaucous, the secondary veins moderately conspicuous, the petiolules 2-4 mm. long, crisp-pubescent; bracts deltoid, about 1 mm. long; flowers 6-7 mm. long; calyx 2-3 mm. long, tomentulose; petal 6-7 mm. long and about 2 mm. wide, cucullate or expanded at anthesis; ovary pubescent along the margin and at the base, otherwise glabrous; fruit mostly glabrous, 2.5-3 cm. long and about 1.3-1.5 cm. broad, the upper margin concave or convex with a wing 1-1.5 mm. wide, sometimes pubescent at the base of the stigma, the stipe puberulous to subglabrous, about 6 mm. long; seed about 6 mm. long, 4 mm. broad, and 1.5 mm. thick, the hilum about 1 mm. long and 0.9 mm. wide.

Distribution: Known from Nayarit and western Jalisco, México, at elevations of 30-450 meters.

MEXICO: NAYARIT: "Dry hill, vicinity of Acaponeta, Tepic," *Rose, Standley, & Russell 14474* (A, F TYPE, GH, NY fragment, US). 1 km. north of El Cuatante, Valle de Banderas, *Rzedowski 17870* (INCB). JALISCO: Soyatán, 30 km. south of Talpa, *Rzedowski 15173* (INCB, US). Sta. Lucía, 7 km. north of Llano Grande, *McVaugh (Feddema) 21275* (MICH).

Local name: Jediondillo (Jalisco).

5. **Ateleia pterocarpa** Moc. & Sessé ex D. Dietr. Syn. Pl. 4: 1219. 1847. Based on *Pterocarpus ateleia* DC. Figure 2.

Ateleia pterocarpa [Sessé & Moc. ex] DC. Prodr. 2: 419. 1825; Lég. Mem. 394. 1826, nomen in synon.

Pterocarpus ateleia DC. Prodr. 2: 419. 1825; Lég. Mem. 394. 1826. TYPE: Plate 288, a painting from the unpublished "Flora Mexicana" of Sessé & Mociño, in the DeCandolle Library (G-DC; F. M. Neg. *30639* ex G-DC). [Lectotype by A. DeCandolle, "Calques des dessins de la Flore du Mexique de Mociño et Sessé qui ont servi des types d'espèces dans le systema ou le prodromus" 2: 288. 1874]. "Habitat in agris Cordovae et in Praedio S. Josephi" (Sessé & Mociño, Fl. Mex. ed. 2, 164. 1894, as *Amorpha.*)

Tree or shrub, to about 7 m. tall; leaves 7-18-foliolate, the axis tomentulose, to about 15 cm. long; leaflets with blades ovate to elliptic, 2-8.7 cm. long, 1-5 cm. broad, obtuse to acute, sometimes retuse, the base rounded or acute, oblique, the upper surface puberulent along the midvein, otherwise glabrous, the lower surface moderately tomentose, glabrescent, the secondary veins moderately conspicuous, the petiolules 2-3 mm. long, tomentulose; bracts deltoid, 1 mm. long; flowers 4-5 mm. long; calyx tomentulose, about 1.5-2 mm. long; petal 4-5 mm. long and 1.5-2 mm. wide, glabrous; ovary glabrous except for some pubescence on the stipe; fruit glabrous, 2-2.3 cm. long, 1-1.2 cm. broad, the wing 1-1.5 mm. wide, the stipe 4-7 mm. long, sometimes pubescent toward the base; seed about 5 mm. long, 3 mm. wide, and about 2 mm. thick.

Distribution: Southern México, in savanna, at elevations of about 200 to 1000 meters.

MEXICO: Without exact locality, presumably Veracruz, "in agris Cordovae" or "in Praedio S. Josephi", *Sessé & Mociño 2017* (F, MA in part).

VERACRUZ: Acatlán, *Salazar s.n.* (US). "Vallée de Cordova," *Bourgeau 1899* (BM, K). Chihuilapan, south of Laguna de Catemaco, Los Tuxtlas, *Sousa 2376* (MEXU, US).

OAXACA: Chivela, *Mell 15* (NY, US fragment). Temascal, *Sousa 1319* (MEXU). Near Presa Alemán, Temascal, *González-Quintero 533* (ENCB, US).

CHIAPAS: Siltepec, *Matuda 1588* (A, K, MEXU, MICH, NY, US). Amatenango del Valle, *Matuda 5833* (LL, MEXU, US), *15833* (F). Pishtimbak, north of Tuxtla Gutierrez, *Miranda 6029* (MEXU, US). Rancho Lindavista, 24 km. east of Villa Flores, *Miranda 5992* (MEXU, US), *6435* (MEXU, US). San Quintín, *Sohns 1639* (MICH, US). Habenal, Tenejapa, *Breedlove 6487* (DS, US), *7644* (DS, ENCB, US).

Local name: Huapinole (Veracruz).

Among Mexican *Ateleia* this species has the smallest

fruit, with the shortest stipes. The pubescent leaflets are similar to those in *A. tomentosa.*

6. **Ateleia tomentosa** Rudd, Contr. U.S. Nat. Herb. **32**: 397. 1968. TYPE: *D. E. Breedlove 11395*, Mexico. Figure 2.

Tree, about 12 m. tall; leaves 9-11-foliolate, the axis tomentose, about 8-12 cm. long; leaflets with blades ovate, 1-6 cm. long and 0.8-3 cm. broad, acute or subacute, the base rounded, usually oblique, the upper surface moderately pubescent, glabrescent, the lower surface tomentose, the secondary venation moderately conspicuous, the petiolules 2-3 mm. long, tomentulose; bracts deltoid, about 1 mm. long; flowers about 6 mm. long; calyx tomentulose, about 2.5 mm. long; petal glabrous, about 6 mm. long and 4-5 mm. wide, somewhat expanded at anthesis; ovary pallid-villous; fruit [submature] tomentose, 2.5-2.8 cm. long and 1.2-1.3 cm. broad, the upper margin straight or concave, the wing about 1 mm. wide, the stipe about 8 mm. long; mature fruit and seed not seen.

Distribution: Known only from the type collection.

MEXICO: CHIAPAS: "Wooded slope 3 miles southwest of Pinola Las Rosas along road to Soyatitán, Municipio of Venustiano Carranza, elevation 4200 feet," *Breedlove 11395* (DS, US TYPE).

The distinctive tomentose fruits distinguish this species from the otherwise similar *A. pterocarpa.*

7. **Ateleia albolutescens** Mohlenbrock, Webbia **17**: 182, fig. 4, 18. 1962. TYPE: *C. A. Purpus 9248*, México. Figure 2.

Tree or shrub, to about 6 m. high; leaves 5-9-foliolate, the axis puberulent, about 6-10 cm. long; leaflets with blades predominantly ovate, sometimes rhombic to suborbicular, 3-7.5 cm. long, 2-5 cm. broad, obtuse to acute, sometimes retuse, the base cuneate, the upper surface puberulent along the midvein, glabrescent, sometimes nitid, the lower surface puberulent with whitish, subappressed hairs, glabrescent, the secondary veins relatively inconspicuous, the petiolules 2-3 mm. long, puberulent; bracts deltoid, about 6 mm. long; flowers about 6 mm. long; calyx tomentulose, 1.5-2 mm. long; petal about 6 mm. long and 2-3 mm. wide; ovary glabrous or ciliate, glabrescent, the stipe usually pubescent; fruit glabrous, 2-2.5 cm. long and 1-1.5 cm. broad, the upper margin convex or almost straight with a wing 1-2 mm. wide, the stipe puberulent, glabrescent, about 5-6 mm. long; seed 4.5-5 mm. long and 3-3.5 mm. wide.

Distribution: Known only from the general area of the type collection, in rocky ravines.

MEXICO: CHIAPAS: Hacienda Monserrate, [southeast of Cintalapa] *Purpus 9248* (F, GH TYPE, NY, UC, US), *10291* (US), *10544* (A, F, NY), *10549* [or *10544?*] (GH, UC), *10577* [or *10544?*] (A). "Tuxtla Gutierrez-Jalisco" [Arriaga], *Purpus 9248* (US).

This species appears to be closely related to *A. pterocarpa* and *A. gummifera*. The various sheets of *Purpus 9248* apparently do not represent a "pure" collection. Material from two different plants can be found on some sheets. The holotype at GH appears to be a mixed sheet, as is one sheet at US bearing a different locality citation.

8. **Ateleia gummifera** (DC.) D. Dietr. Syn. Pl. **4**: 1219. 1847. Figure 2.

Pterocarpus gummifer Bert. ex DC. Prodr. **2**: 419. 1825; Mém. 395, pl. 57, f. 1. 1826. TYPE: *C. G. L. Bertero s.n.*, "S. Doming.," Dominican Republic.

Dalbergia gummifera Spreng. ex DC. Mém. Leg. 395. 1826, nomen in synon.

Swartzia multijuga A. Rich. Essai Flor. Cuba 457. 1846; in Sagra, Hist. Fis., Pol., y Nat. Cuba **10**: 201. 1846; 12: tab. 42. 1846, non Vog. 1837. TYPE: *R. de la Sagra*?, Cuba.

Ateleia cubensis Griseb. Mem. Am. Acad. N.S. **8**: 180. 1860, nom. nov. for *Swartzia multijuga* A. Rich.

Ateleia multijuga (A. Rich.) A. S. Hitch. Rep. Mo. Bot. Gard. **4**: 80. 1893.

Ateleia tumida Mohlenbrock, Webbia **17**: 166, fig. 3, 10. 1962. TYPE: *M. Fuertes s.n.*, Dominican Republic.

Ateleia gummifera var. *cubensis* (Griseb.) Mohlenbrock, Webbia 17: 172. 1962.

Ateleia parvifolia Mohlenbrock, Webbia **17**: 174. 1962. TYPE: *E. Ekman 7532*, Cuba.

Shrub or small tree, to about 7 m. tall; leaves 5-13-foliolate, the axis puberulent, glabrescent, about 5-10 cm. long; leaflets with blades elliptic, rhombic, oblong, obovate, or ovate, 1-8 cm. long, 0.5-3.5 cm. broad, obtuse to subacute, sometimes retuse, the base cuneate to obtuse, the surfaces usually glabrous at maturity, sometimes pubescent, especially along the midvein, the hairs appressed or crispate, the secondary veins usually inconspicuous, the petiolules 2 mm. long or less, puberulent, glabrescent; bracts deltoid, commonly 1 mm. long; bracteoles apparently lacking; flowers 5-6 mm. long; calyx tomentulose, sometimes glabrescent, 2-3 mm. long; petal 5-6 mm. long, 2-4 mm. wide, cucullate, sometimes expanded at anthesis; ovary puberulent along the margin and at the base, otherwise glabrous; fruit glabrous, 2-3.5 cm. long and 1-1.5 cm. broad, the upper margin with

a wing 1-2 mm. wide, the stipe 0.5-1.3 cm. long, puberulent or glabrous; seed 5-7 mm. long, 3-3.5 mm. broad, and about 2 mm. thick, the hilum 1 mm. in diameter.

Distribution: México, northern Central America, and the West Indies, at elevations from about sea level to 1000 meters.

MEXICO: CAMPECHE: Tuxpeña, Lundell *849* (A, DS, GH, K, MICH, NY, UC, US), *862* (DS, GH, MICH, NY, UC, US).

Local names: Balsamo hediondo, cerezo (Cuba); tush che (British Honduras).

This species is relatively wide-ranging and exhibits considerable variation, especially in shape and pubescence of leaflets; most specimens have glabrous or sparsely appressed-pubescent leaflets but those from the Yucatan peninsula, eastern Cuba, and Hispaniola tend toward crisp-pubescence.

5. DUSSIA Krug and Urban ex Taubert

Dussia Krug and Urban ex Taubert in Engler and Prantl, Natürl. Pflanzenfam. 3, Abt. 3: 193. 1892. TYPE: *D. martinicensis* Krug & Urban ex Taubert. Martinique.

Vexillifera Ducke. Arch. Jard. Bot. Rio de Janeiro 3: 139. 1922. TYPE: *V. micranthera* Ducke. Brazil.

Cashalia Standley, Journ. Wash. Acad. Sci. 13: 440. 1923. TYPE: *C. cuscatlanica* Standl. El Salvador.

Reference: V. E. Rudd, Contr. U.S. Nat. Herb. 32: 247-277. 1963.

Trees, unarmed; leaves alternate, imparipinnate; leaflets alternate or subopposite; stipules and stipels apparently lacking; inflorescences pseudoterminal, racemose; flowers of medium size, about 15-25 mm. long; calyx campanulate, somewhat oblique with 5 subequal teeth or lobes; corolla papilionaceous with 5 separate petals, pink to purple, the standard pubescent on the outer face; stamens 10, subequal, the filaments essentially separate to the base, or with some adhesion near the base in groups of two to four, the anthers uniform, small, ellipsoid, seeds red, ellipsoid or subcylindrical, the hilum linear, subapical or lateral.

About 10 species, in tropical America.

KEY TO SPECIES OF DUSSIA

Leaves 5-15-foliolate, the axis about 15-60 cm. long, the leaflets ovate, oblong, or obovate, obtuse or acute, or sometimes acuminate, 3-26 cm. long; bracts lanceolate, entire, the apex acute or acuminate, 5-9 mm. long and 0.5-2 mm. wide; bracteoles lanceolate, entire, obtuse or acute, 3-4 mm. long and 0.5-1 mm. wide (Veracruz) .... 1. *D. mexicana*

Leaves 11-25-foliolate, the axis about 30-100 cm. long, the leaflets mostly oblong, acuminate, 7-35 cm. long; bracts tridentate to rhombic or lanceolate, erose or entire, 5-10 mm. long and 2-4 mm. wide; bracteoles ovate, entire or dentate, acuminate, 5-7 mm. long and 2-3 mm. wide (Chiapas) .... 2. *D. cuscatlanica*

1. **Dussia mexicana** (Standl.) Harms, Repert. Sp. Nov. **19**: 294. 1924. Figure 1.

Ormosia mexicana Standl. Contrib. U.S. Nat. Herb. **23**: 436. 1922. TYPE: *C. A. Purpus 6326*. Mexico.

Tree, to about 40 m. high; leaves 5-15-foliolate, the axis about 15-60 cm. long, fulvo-tomentulose, glabrescent, the leaflets alternate or subopposite, the blades 3-26 cm. long, 2-10 cm. broad, ovate to oblong, the terminal leaflet usually obovate, the apex predominantly obtuse, acute or sometimes acuminate, the acumen to about 12 mm. long, the base obtuse to subcordate, often oblique, the upper surface glabrous, the lower surface moderately puberulent with patent or subpatent hairs or somewhat crispate along the major veins, the venation moderately conspicuous, sometimes darkening on drying, the tertiary veins scalariform; inflorescences with axes ferrugino-tomentose, the bracts lanceolate, acute to acuminate, 5-9 mm. long, 0.5-2 mm. broad, the bracteoles lanceolate, obtuse to acute, 3-4 mm. long and 0.5-1 mm wide; flowers 18-22 mm. long; calyx ferrugino-tomentulose, 8-10 mm. long, the tube 5-6 mm. long, the teeth 3-4 mm. long; petals pink with white pubescence; fruit minutely fulvo-velutinous, 1- or 2-seeded, 5-6 cm. long and about 2.5 cm. broad; seeds not seen but, presumably, like those of *D. cuscatlanica.*

Distribution: Known only from the state of Veracruz, in humid forest.

MEXICO: VERACRUZ: Zacuapan, *Purpus 6326* (BM, GH, MO, NY, UC, US TYPE of *Ormosia mexicana*). El Mirador, *Purpus 277* (A), *16459* (A, F, K, US); *Leibmann 5355* (C, F). Zontecomapan, *Andrle & Axtell 5* (US). Tapalapan, *Andrle 91* (US). Camino Misantla-Yecuatla, *Gómez-Pompa 952* (MEXU, US), *1162* (MEXU). Cochinitos, Coyame, NE. Laguna de Catemaco, *Sousa 2775* (MEXU, US).

Local names: Frijolillo, jaboncillo, palo de zopilote.

It is possible that this and the next species should be synonymous. The differences are weak and, without knowing the locality of origin of a specimen, it is often difficult to decide which name should be applied.

2. **Dussia cuscatlanica** (Standl.) Standl. & Steyermark, Field Mus. Pub. Bot. **22**: 341. 1940. Figure 1.
Cashalia cuscatlanica Standl. Journ. Wash. Acad. Sci. **13**: 441. 1923. TYPE: *P. C. Standley 20197.* El Salvador.
Dussia grandifrons Johnst. Journ. Arn. Arb. **19**: 118. 1938. TYPE: *A. F. Skutch 2027.* Guatemala.

Tree, to about 50 m. high; leaves 11-25-foliolate, the axis about 30-100 cm. long, fulvo- or ferrugino-pubescent with crispate or somewhat patent hairs, the leaflets alternate or subopposite, the blades 7-35 cm. long, 2.5-9 cm. broad, commonly oblong, sometimes ovate or obovate, the apex acuminate to acute, the base obtuse, truncate, or subcordate, the upper surface glabrous, the lower surface moderately pubescent with subpatent or crispate hairs, the venation moderately conspicuous, the tertiary venation scalariform; bracts tridentate to rhombic, or lanceolate, erose or entire, acuminate, 5-10 mm. long, 2-4 mm. broad; bracteoles obovate, entire or dentate, acuminate, 5-7 mm. long and 2-3 mm. broad; flowers (15-) 18-25 mm. long; calyx ferrugino-tomentulose, 8-10 mm. long, the tube and teeth about equal in length; petals pink with greenish or purplish markings and white pubescence; fruit fulvo-velutinous, 1- or 2-seeded, 5-10 cm. long, 2.5-3.5 cm. broad and about 1.5-2 cm. thick; seeds about 2-3.5 cm. long and 1.3-1.7 mm. in diameter.

Distribution: In forest, southern Mexico to Costa Rica, at elevations of 20-2000 meters.

MEXICO: CHIAPAS: Near Finca Prusia, south of Jaltenango, *Miranda 6964* (MEXU, US). Esperanza, Escuintla, *Matuda 18585* (MEXU). La Grada, Acacoyagua, *Matuda 18640* (MEXU).

Local names: Cedillo, matabuey (México); cashal (El Salvador); cereza de montaña, garvancillo de montaña, palo de tigre (Guatemala).

In El Salvador the trees of this species are cut for lumber.

6. ORMOSIA Jackson

Ormosia Jacks. Trans Linn. Soc. Lond. **10**: 360, t. 25-27. 1811, nom. conserv. TYPE: *Robinia coccinea* Aubl. French Guiana.

Toulichiba Adans. Fam. 2: 326. 1763, nom. rejec. Monomial.

Ormosiopsis Ducke, Arch. Jard. Rio de Janeiro **4**: 61. 1925. TYPE: *Clathrotropis* (?) *flava* Ducke. Brazil.

Macroule Pierce, Trop. Woods **71**: 2. 1942. TYPE: *Ormosia coutinhoi* Ducke. Brazil.

Reference: V. E. Rudd, Contrib. U.S. Nat. Herb. **32**: 279-384. 1965.

Trees, unarmed; leaves alternate, imparipinnate; leaflets opposite; stipules small, deltoid to linear, caducous, apparently lacking in some species; stipels usually lacking, occasionally present in some species; inflorescences terminal or pseudoterminal, racemose; flowers small to medium in size, about 6-25 mm. long; calyx campanulate, hypanthoid, with 5 subequal teeth or lobes; corolla papilionaceous with 5 separate petals, yellow to blackish purple, the standard glabrous on the outer face; stamens normally 10, alternately subequal, the smaller sometimes sterile or lacking, the filaments separate to the base, the fertile anthers small, ellipsoid, dorsifixed; stigma bilobed, usually lateral; fruit commonly dehiscent, a few species indehiscent, glabrous to velutinous, moderately compressed, 1-6 seeded; seeds [Mexican species] red or bicolored red and black, subglobose, the hilum apical, elliptic.

About 100 species, with 50 in tropical America.

KEY TO SPECIES OF ORMOSIA.

Leaflets glabrous on both surfaces with about 5-9 pairs of secondary veins only approximately parallel, arcuate, irregularly spaced; fruit coriaceous, finely pubescent, glabrescent; seeds red (Veracruz; Tabasco) .... 1. *O. macrocalyx*

Leaflets pubescent or subglabrous below with about 10-15 pairs of secondary veins, essentially parallel and regularly spaced; fruit lignous, glabrous or nearly so; seeds red or red and black.

Seeds red; fruit glabrous, nitid or subnitid; flowers about 10 mm. long; leaflets with lower surface finely velutinous along the major veins, otherwise finely and sparsely appressed-pubescent (Oaxaca) .... 2. *O. isthmensis*

Seeds red and black; fruit essentially glabrous at maturity but often with a trace of pubescence at the base; flowers 18-22 mm. long; leaflets with lower surface loosely crisp-pubescent (Chiapas) .... 3. *O. schippii*

1. **Ormosia macrocalyx** Ducke, Arch. Jard. Bot. Rio de Janeiro **3:** 137. 1922. TYPE: *A. Ducke 7345*. Brazil. Figure 1

Ormosia apulensis Cortés, Flora de Colombia, 61. 1919, nomen nudum. TYPE *J. J. Triana 4336*. Colombia.

Ormosia toledoana Standl. Carnegie Inst. Publ. **461:** 64. 1935. TYPE: *W. A. Schipp 1052*. British Honduras.

Ormosia chlorocalyx Ducke, Bol. Téc. Inst. Agron. Belém, **2:** 23. 1944. TYPE: *A. Ducke 1516*. Brazil.

Tree, to about 40 m. high; stipules linear, about 5 mm. long, caducous; leaves 7-11-foliolate, the axis 10-45 cm. long, sparsely pubescent, glabrate, the leaflets with blades coriaceous to subcoriaceous, ovate to ovate-oblong, 6-19 cm. long, 3-9 cm. broad, the apex obtuse to breviacuminate, the base rounded to subcordate, the upper surface glabrous, nitid or subnitid, the lower surface glabrous, the secondary veins inconspicuous; bracts linear, 3-10 mm. long, 1 mm. broad or less; bracteoles subulate, 1-1.5 mm. long; flowers 18-25 mm. long; calyx 8-15 mm. long, pubescent with gray, subappressed hairs, the tube (3-) 8-10 mm. long, the teeth 3-5 mm. long; petals lilac to dark purple; fruit dehiscent, coriaceous, black or brown, glabrescent but often with some fine, fulvous pubescence at maturity, 1-6- (commonly 2- or 3-) seeded, 3-10 cm. long, 2-3.5 cm. broad, slightly constricted between the seeds, 10-15 mm. thick; seeds red, lustrous, 10-13 mm. long, 10 mm. broad, and 7-8 mm. thick.

Distribution: In wet, swampy forest, southern México to the Amazon basin of Brazil, at elevations up to about 100 meters.

MEXICO: VERACRUZ: Fortuño, Río Coatzacoalcos, *Ll. Williams 8926* (F, G, K, S, U, US). Fortuño, Río Coachapa, *Gómez-Pompa 114* (MEXU).

TABASCO: Cocoital, Comalcalco, *Guzmán* s.n. (US).

Local names: Colorín, caracolillo (México); alcornoque, casique, pernilla del monte (Panamá); chocho grande (Colombia); tento (Brazil); huyruro (Peru).

2. **Ormosia isthmensis** Standl. Publ. Field Mus. Bot. **17:** 264. 1937. TYPE: *Ll. Williams 9123*. México. Figure 1

Tree, to about 50 m. tall; stipules deltoid, acicular, about 1-2 mm. long, 1-1.5 mm. broad at the base, pubescent; leaves (3-5-) 7-13-foliolate, the axis 9-45 cm. long, pubescent, glabrescent; leaflets with blades coriaceous, ovate, oblong to obovate-oblong, 3-35 cm. long, 2-10

cm. broad, acute to abruptly acuminate, the acumen to about 10 mm. long, the base obtuse or truncate, the upper surface glabrous, subnitid or nitid, the lower surface finely velutinous along the major veins, otherwise finely and sparsely appressed-pubescent, glabrescent, the secondary veins about 10-12 pairs, moderately raised; bracts and bracteoles linear, 2-3 mm. long; flowers about 10 mm. long; calyx cano- to fulvo-velutinous, 7-8 mm. long, the tube 3-4 mm. long, the teeth about 4 mm. long; petals pink-purplish with white markings; fruit dehiscent, lignous, black or dark brown, glabrous, nitid or subnitid, 1-3, commonly 1-seeded, 3-7 cm. long, 2-3 cm. broad; seeds red, 10-13 mm. long, 8-11 mm. wide, and 6-8 mm. thick.

Distribution: In rain forest, from southern México to northern Colombia, at elevations of about 5-800 meters.

MEXICO: OAXACA: Ubero, *Ll. Williams 9423* (BM, F TYPE, G, K, MICH, S, US). Santiago Yaves, Choapan, *Reko 9* (F). San Juan Lalana, Choapan, *Schultes & Reko 822* (F, GH, NA, UC). Sierra Juarez, *Gómez-Pompa, Sharp, & Hernandez 380* (MEXU, MICH, RSA, UC, US). "Arriba de Valle Nacional, rumbo a Oaxaca," *Gómez-Pompa 5* (MEXU).
TABASCO: Huimanguillo, *Chavelas & Gonzalez 134* (MEXU); *Barlow 30/99* (MICH).

Local names: Colorín, mū-sa, palo de Salvador, frijolillo (México); acu-té (Guatemala); hormiga (British Honduras); alasán (Costa Rica).

3. **Ormosia schippii** Pierce ex Standl. and Steyerm., emend Rudd, Trop. Woods No. **113**: 125. 1960. TYPE: *W. A. Schipp 1297*. British Honduras. Figure 1
Ormosia schippii Pierce ex Standl. & Steyerm. Fieldiana Bot. **24 (5)**: 311. 1946, pro parte.

Tree, to about 35-40 m. high; stipules not seen; leaves 5-9-foliolate, the axis 10-35 cm. long, tomentulose, glabrescent, the blades coriaceous or subcoriaceous, ovate to ovate-oblong or sometimes obovate, 5-27 cm. long, 3-11 cm. wide, the apex acute or breviacuminate, the acumen to about 10 mm. long, the base obtuse to subcordate, the upper surface glabrous except for a trace of pubescence along the major veins, the lower suface moderately pubescent, the hairs loosely crispate, the secondary veins raised; bracts lanceolate, acuminate, 8-10 mm. long, 2-2.5 mm. broad; bracteoles linear, 7-8 mm. long, 1 mm. broad; flowers 18-22 mm. long; calyx cinereo- to fulvo-tomentulose, 7-10 mm. long, the tube 4-5 mm. long, the teeth 3-5 mm. long; petals reddish

purple; fruit dehiscent, sublignous, black or dark brown, essentially glabrous at maturity but often with a trace of pubescence at the base, commonly 1-seeded, 2-3 cm. long, 2-2.5 cm. broad, about 1.5 cm. thick; seeds bicolored, red and black, 12-13 mm. long, 10-12 mm. broad, and 7-9 mm. thick.

Distribution: In rain forest, generally in swampy places, southern México and British Honduras, at elevations up to about 150 meters.

MEXICO: CHIAPAS: Selva Lacandona, *Gómez-Pompa 339* (MEXU, US). Between La Arena and Salas, *Miranda 8471/1* (MEXU). CAMPECHE: Campo Experimental El Tormento, Escárcega, *Marroquin s.n.* (MEXU).

Local names: Palo macho, carne de caballo (Chiapas); bayo, yabo (Campeche); John Crow bead (British Honduras).

7. SOPHORA L.

Sophora L. Sp. Pl. 373. 1753. LECTOTYPE: *S. alopecuroides* L. (Britton & Brown, Ill. Fl. N. U. S. ed. 2, 2: 342. 1913). "Oriente."

Broussonetia Gómez-Ortega, Hort. Matr. Dec. 61. 1798, nom. rej., non L'Hér. ex Vent. 1799, nom. cons. TYPE: *B. secundiflora* Gómez-Ortega. Cultivated, ex México.

Patrinia Raf. Journ. Phys. Chim. Hist. Nat. 89: 97. 1819, non Juss. 1807. TYPE: *Sophora sericea* Nutt. South Dakota.

Sophora sect. *Eusophora* DC. Prodr. 2: 95. 1825. Based on 10 species, including *S. tomentosa* L.

Sophora sect. *Pseudosophora* DC. Prodr. 2: 96. 1825. TYPE: *S. alopecuroides* L. "Oriente."

Pseudosophora (DC.) Sweet, Hort. Brit. ed. 2. 122. 1830.

Styphnolobium Schott, Wien. Zeitschr. 3: 844. 1830. TYPE: *Sophora japonica* L. Japan.

Vexibia Raf. Neogen. 3. 1825; Atlantic Journ. 144. 1832, nom. nov. for *Patrinia* Raf.

Calia Berlandier in Mier-Terán, Mem. Comisión Limites 13. 1832. TYPE: *C. erythrosperma* Berlandier. Texas and Mexico.

Zanthyrsis Raf. New Fl. 3: 84. 1838. TYPE: *Z. paniculata* Raf. South Florida and Cuba.

Agastianis Raf. New Fl. 3: 85. 1838, nom. nov. for *Broussonetia* Gómez-Ortega.

Dermatophyllum Scheele, Linnaea 21: 458. 1848. TYPE: *D. speciosum* Scheele. Texas.

Vibexia Raf. ex Jacks. Index Kew. 2: 1193. 1895, error for *Vexibia* Raf.

Trees, shrubs, or perennial herbs; leaves alternate, imparipinnate; leaflets alternate to opposite; stipules commonly deltoid, sometimes lacking; stipels lacking in Mexican species; inflorescences terminal or sometimes axillary, racemose or paniculate; flowers small to medium in size, about 1-4.5 cm. long; calyx campanulate with 5 subequal lobes, sometimes subtruncate; corolla papilionaceous, yellow, white, or blue to violet, glabrous, the keel petals commonly joined; stamens 10, free or the filaments united at the base, alternately subequal; anthers ellipsoid, dorsifixed, about 1 mm. long; stigma minutely capitate-penicillate; fruit commonly indehiscent, 1-6 (-15) seeded, somewhat torulose; seeds spherical or subellipsoid, red or yellowish to light brown, the hilum lateral or subapical, elliptic or orbicular.

About 75 species, worldwide in tropical and temperate regions.

The generic lectotype, *S. alopecuroides,* designated by Britton and Brown, has been accepted for the Index Genericorum. Presumably, that species was chosen from six assigned to *Sophora* in the first edition of Species Plantarum because it alone was cited by Linnaeus in his earlier work, Hortus Cliffortianus, and represented his original concept of the genus.

However, Hitchcock and Green (in Proposals by British Botanists 111-119. 1929; Brittonia 6: 117. 1947) and Hutchinson (The Genera of Flowering Plants 1: 328. 1964) have considered *S. tomentosa* L. to be the type of *Sophora,* a view that I favor in the light of DeCandolle's and, later, Sweet's treatments of the genus. As shown in the above list of synonymy, DeCandolle selected *S. alopecuroides* as the one discordant species to be segregated into his section *Pseudosophora,* in contrast to the ten species, including *S. tomentosa,* placed in section *Eusophora.* A few years later, Sweet raised *Pseudosophora* to generic status. Thus, we have the incongruous situation that, if the generic concept of Sweet and the typification of Britton and Brown be followed, *Pseudosophora* would be reduced to *Sophora,* the prior synonym, and the true *Sophora* sensu DeCandolle, would have to be transferred to such later, synonymous genera as *Styphnolobium, Calea,* and *Zanthyrsis.* Fortunately, except for *Styphnolobium,* which is sometimes

recognized as a separate genus, the others are commonly retained as synonyms of *Sophora,* sensu latior.

KEY TO SPECIES OF SOPHORA.

Plants herbaceous from a woody root, to about 30 cm. high; flowers 15-20 mm. long; fruit about 5 mm. in diameter (Coahuila; Chihuahua; San Luis Potosí) .... 1. *S. nuttalliana*

Plants woody, shrubs or trees, about 3-12 m. high; flowers 20-30 mm. long; fruit 8-20 mm. in diameter (not known in *S. conzattii*).

Calyx about 6 mm. long, subtruncate; corolla with keel petals separate (Oaxaca) .... 4. *S. conzattii*

Calyx 10-15 mm. long, subtruncate to lobed; corolla with keel petals joined.

Fruit (10-) 15-20 mm. in diameter; calyx 10-15 mm. long with lobes 3-5 mm. long (Coahuila; Nuevo León; Tamaulipas; Zacatecas; San Luis Potosí) .... 5. *S. secundiflora*

Fruit 8-10 mm. in diameter; calyx 10 mm. long with teeth 1 mm. long or less.

Flowers about 20 mm. long; calyx with teeth about 1 mm. long (Coahuila; Zacatecas) .... 2. *S. purpusii*

Flowers about 25 mm. long; calyx subtruncate (Clarion Isl., Baja California, Tamaulipas; Yucatan; Quintana Roo, Cozumel Isl.) .... 3. *S. tomentosa*

A cultivated species, *Sophora japonica* L., has not been included in the key.

1. **Sophora nuttalliana** Turner, Field and Lab. **24:** 15. 1956, nom. nov. for *S. sericea* Nutt. Figure 3

Sophora sericea Nutt. Gen. Pl. **1:** 280. 1818, non Andrews 1806. TYPE: *T. Nuttall s.n.,* South Dakota.

Patrinia sericea (Nutt.) Raf. Journ. Phys. Chim. Hist. Nat. **89:** 97. 1819.

Pseudosophora sericea (Nutt.) Sweet, Hort. Brit. ed. 2. 122. 1830.

Vexibia sericea (Nutt.) Raf. Atlan. Journ. 144. 1832.

Vibexia sericea (Nutt.) Raf. ex Jacks. Ind. Kew. **2:** 1193. 1895, error for *Vexibia sericea.*

Herb, perennial from woody root, commonly 10-30 cm. high; stems pubescent with white, subappressed, antrorse hairs; stipules deltoid, sericeous, 1-5 mm. long, 0.2-2 mm. broad at the base, caducous; leaves 7-25-foliolate, the axis about 3-8 cm. long, white sericeous, the lateral leaflets alternate to subopposite, the blades elliptic or ovate, 3-15 mm. long, 2-10 mm. broad, the apex obtuse, sometimes emarginate, the base obtuse to cuneate, the upper surface essentially glabrous, the lower surface sericeous, the secondary venation not evident; bracts

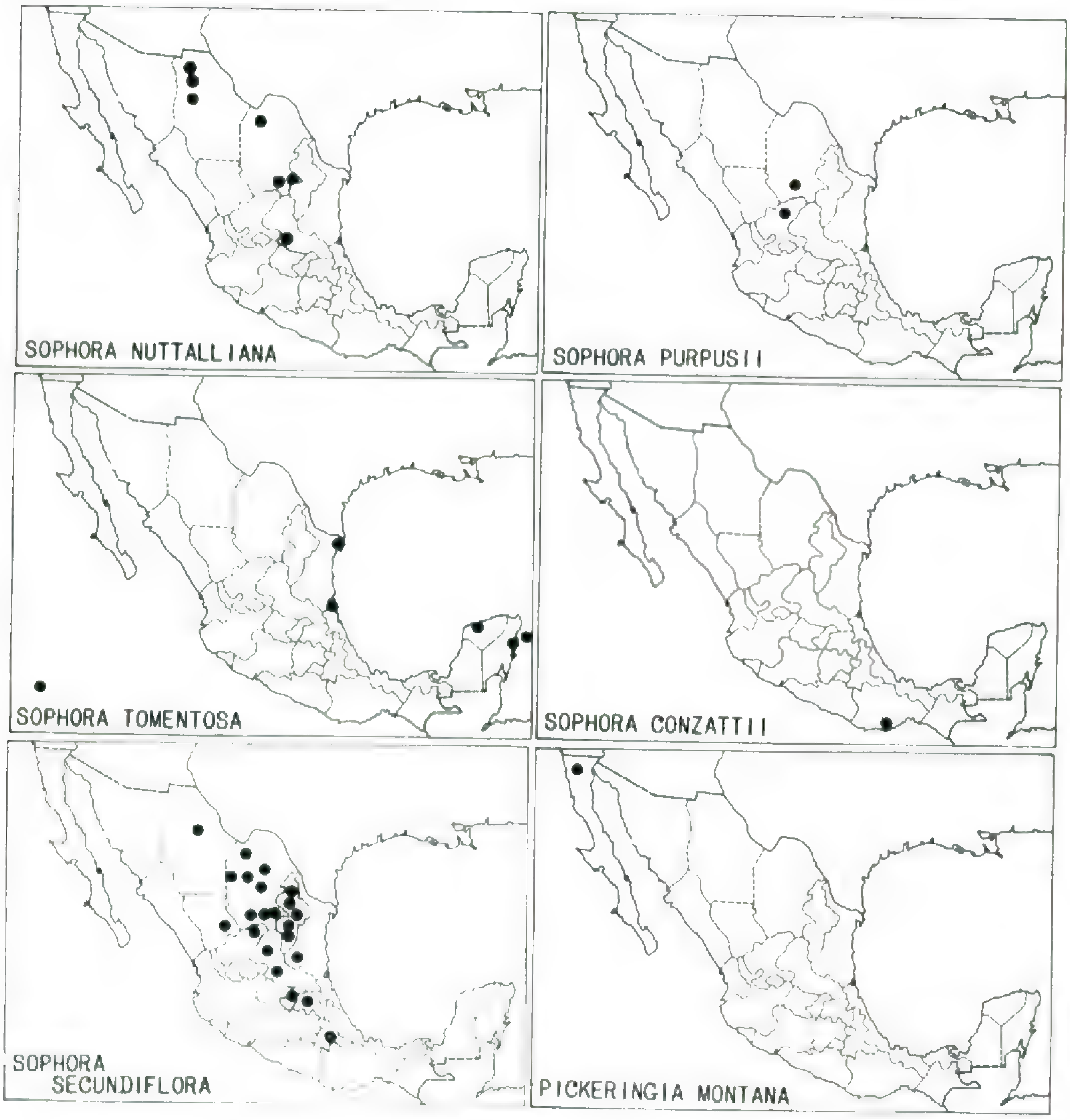

Fig. 3. Geographic distribution of *Sophora* and *Pickeringia* in Mexico.

at base of pedicels linear-deltoid, sericeous, 3-5 mm. long; bracteoles apparently lacking; flowers about 15-20 mm. long; calyx subsericeous, sometimes purplish, somewhat gibbous, 6-9 mm. long, the tube 4-7 mm. long, the teeth deltoid, about 2 mm. long; corolla whitish, the standard reflexed, about one fourth longer than the wings and keel, the keel petals united toward the apex; fruit coriaceous, stramineous, sericeous, glabrescent, terete, torulose, 1-6-seeded, about 2-5 cm. long, 5 mm. in diameter at the seeds, the apex usually attenuate; seeds sublustrous, yellowish to light brown with a darker line along the chalazal side, ellipsoid, about 5 mm. long and 3 mm. in diameter, the hilum lateral, subapical, orbicular, about 0.2 mm. in diameter.

Distribution: Prairie and rocky hillsides up to about 3000 m. elevation, South Dakota and Wyoming to Arizona and northern Mexico.

MEXICO: COAHUILA: Lirios, *Palmer 264* in 1880 (GH, NY, US). Rancho Los Angeles, about 40 km. SW. of Saltillo, *Gould & Watson 10503* (MICH).

COAHUILA ? : Las Vegas, *Arsène 18963* (F), *18526* (F).

CHIHUAHUA: Madera, *Palmer 266* in 1908 (F, GH, NY, US). Rio Grande Valley, *Pringle 5366* (MEXU, US), *s.n.*, June 16, 1885 (GH). Paseo del Norte, *Pringle 107* (GH), *5233* (MEXU, US). San Ysidro, SW. of Barranca, *Mexia 2526* (BM, CAS, GH, MICH, POM, NY, UC, US). Janos to Guadeloupe Cañon, *E. K. Smith s.n.* (NY). Below high ridge crests at NW. end of Sierro del Diablo, *Stewart 998* (GH).

SAN LUIS POTOSÍ: San Luis Potosí, *Parry & Palmer 199* (BM, GH, NY, US).

Local names: Frijolillo (México); white loco, silky sophora (United States).

2. **Sophora purpusii** Brandeg. Zoe 5: 235. 1906. TYPE: *C. A. Purpus 1076*. México. Figure 3

Shrub; stipules deltoid, sericeous, 1-2 mm. long, caducous; leaves 13-19-foliolate, the axis about 3-5 cm. long, white-velutinous, the lateral leaflets essentially opposite, the blades coriaceous, orbiculate, oblong, or obovate, about 5-8 mm. long, 3-5 mm. broad, the apex obtuse or emarginate, the base rounded, the upper surface moderately appressed-pubescent, glabrescent, nitid, the lower surface sericeous, the secondary veins not evident; bracts at base of pedicels, deltoid, 1-2 mm. long; paired bracteoles subtending the calyx, minute, pubescent; flowers about 20 mm. long; calyx subsericeous, 10 mm. long, the teeth deltoid, about 1 mm. long, the tube about 9 mm. long; corolla white with purplish markings, the standard a little longer than the wings and keel; fruit coriaceous, sericeous, glabrescent, compressed, somewhat torulose, 1-6-seeded, about 4-6 cm. long, 8-10 mm. broad at the seeds, the apex acute; seeds not seen.

Distribution: Known only from Coahuila and Zacatecas, México.

MEXICO: COAHUILA: Sierra de Parrás, *Purpus 1076* (F, GH, NY, POM, UC TYPE, US). Dry valley east of Parrás, *without collector's name*, April 11/47 (GH).

ZACATECAS: North of San Lucas, *Lloyd 29* (K, UC, US). Cedros, *Lloyd 141* (GH).

Local name: Frijolillo.

3. **Sophora tomentosa** L. Sp. Pl. 373. 1753, non Hort. ex Dippel. 1893. TYPE: *P. Hermann s.n.* Ceylon. Figure 3

Sophora occidentalis L. Syst. ed. 10, 1015. 1759. TYPE: *P. Browne s.n.* Jamaica.

Sophora havanensis Jacq. Enum. Pl. Carib. 20. 1760. TYPE: *N.J. Jacquin s.n.* Cuba.

Sophora littoralis Schrad. in Goett. Gel. Anz. 1: 709. 1821. TYPE: *M. Wied-Neuwied s.n.* Brazil.

Sophora arenicola Nees, Flora 4: 297. 1821. TYPE: *M. Wied-Neuwied s.n.* Brazil.

Zanthyrsis paniculata Raf. New Fl. 3: 84. 1838. TYPE: *Z. Collins s.n.* Florida or Cuba.

Sophora tomentosa L. β *truncata* Torr. & Gray, Fl. N. Am. 1: 389. 1840. TYPE: *"Dr. Hulse, Dr. Leavenworth."* Florida.

Sophora tomentosa L. β var. *littoralis* (Schrad.) Benth. in Mart. Fl. Bras. 15(1): 330, t. 124. 1862.

Shrub, to about 3 m. high; stipules linear-deltoid, tomentulose, about 3 mm. long, caducous; leaves 13-21-foliolate, the axis about 12-25 cm. long, puberulent, the lateral leaflets opposite or subopposite, the blades oblong, orbicular, ovate, or obovate, commonly suborbicular, about 2-6 cm. long, 1-4 cm. broad, the apex obtuse, cuneate, or subcordate, the upper surface sericeous to glabrous, sometimes nitid, the lower surface sericeous or puberulent, the secondary venation inconspicuous; bracts linear, 3-5 mm. long; bracteoles apparently lacking; flowers about 25 mm. long; calyx pallid-sericeous, about 10 mm. long, subtruncate; petals white to yellow, the standard a little longer than the other petals; fruit subcoriaceous, cinereo-tomentulose, terete, torulose or moniliform, 1-15-seeded, 5-15 cm. long and about 8 mm. in diameter at the seeds; seeds sublustrous, light-brownish, spherical or subellipsoid, 5-8 mm. long, 5-6 mm. in diameter.

Distribution: Pantropical, usually near the sea, frequently on [restricted to ?] limestone.

MEXICO: Without exact locality, *Sessé & Mociño 1072* (F); "Mex. boundary," *Schott s.n.* (F).

BAJA CALIFORNIA: Clarion Isl., *Anthony 404* (DS, GH, US); *Barkelew 246* (GH, UC); *Barclay s.n.* (K); *Solis 6* (US), *3602* (MEXU); *Mason 1562* (CAS, GH, K, US); *Townsend s.n.* in 1889 (US); *Elmore B4* (DS,

F, GH, NY, UC, US); *Howell 8374* (CAS, DS, GH, K, NY, POM, UC, US); *Craig 583* (POM); *Carlquist 393* (RSA); *Cárdenas s.n.* (ENCB).

TAMAULIPAS: Washington Beach, *Runyon 473* (NY, US). Coastal dunes near Rio Grande, *LeSueur 206* (F, GH). Brasos Santiago, *Schott 289a* (NY). Barra de Tampico, *Maury 6489* (MEXU).

YUCATAN: Chuburná, *Enríquez 683* (MEXU, US).

QUINTANA ROO: Tancah, *Steere 2512* (F, MICH). Cozumel Isl., San Miguel, *Steere 2955* (F); *Rudd 2035* (US).

Local name: Xoxoak (Mexico); tambalisa (Cuba).

This species was reported from Socorro Isl. (*Barkelew 246*) but the collection probably was made on Clarion Isl. according to I. M. Johnston (Proc. Calif. Acad. Sci. ser. 4, **20**: 14, 64. 1931).

4. **Sophora conzattii** Standl. Contrib. U.S. Nat. Herb. **23**: 436. 1922.
TYPE: *C. Conzatti, B. P. Reko, & E. Makrinius 3171*. México.
Figure 3

Tree; stipules not seen; leaves 7-9-foliolate, the axis 9.5-13 cm. long, puberulent, glabrate, the lateral leaflets essentially opposite, the blades coriaceous, ovate or elliptic-ovate, 3.5-5.5 cm. long, 2.2-3.5 cm. broad, the apex obtuse or subacute, the base obtuse, the surfaces glabrous, the secondary venation reticulate, fairly prominent; inflorescences axillary; bracts deltoid, about 1 mm. long, caducous; bracteoles minute, caducous; flowers 20-25 mm. long; calyx ferrugino-sericeous, subtruncate, about 6 mm. long; petals violet, separate, the standard reflexed, a little longer than the wings and keel petals; ovary pallid-sericeous, the style pubescent toward the base, glabrous toward the apex; fruit and seed not known.

Distribution: Known only from the type.

MEXICO: OAXACA: "Cerro Espina," Pochutla, at 1200 m. elevation, *Conzatti, Reko & Makrinius 3171* (US).

Local name: Frijolillo.

I am not fully convinced that this species is a *Sophora* but until a fruiting specimen can be examined I have no other suggestion. The leaflets closely resemble those of *Sweetia panamensis*. The flowers with separate petals

resemble those of *Ormosia* but lack the characteristic bilobed stigma of that genus.

5. **Sophora secundiflora** (Gómez-Ortega) Lag. in DC. Cat. Hort. Monsp. 148. 1813. Figure 3

Broussonetia secundiflora Gómez-Ortega, Hort. Matr. Dec. 61, pl. 7. 1798. LECTOTYPE: *M. Lagasca s.n.* Cultivated Botanical Garden, Madrid, ex Mexico ("è seminibus missis per D. sessé") (Designated by R. McVaugh in herb. G-DC).

Virgilia secundiflora (Gómez-Ortega) Cav. Ic. 5: 1, pl. 401. 1799.

Calia erythrosperma Berlandier in Mier-Terán, Mem. Comisión Limites 13. 1832. TYPE: *J. L. Berlandier s.n.* (?). Texas and México.

Agastianis secundiflora (Gómez-Ortega) Raf. New Fl. 3: 86. 1838.

Dermatophyllum speciosum Scheele, Linnaea **21**: 459. 1848. TYPE: *R. Römer s.n.* Texas.

Sophora speciosa (Scheele) Benth. in A. Gray, Boston Journ. Nat. Hist. **6**: 178. 1850, non Torr. 1856.

Sophora sempervirens Engelm. in A. Gray, Boston Journ. Nat. Hist. **6**: 178. 1850, nomen in synon.

Cladrastis secundiflora (Gómez-Ortega) Raf. ex Jacks. Index Kew. **1**: 552. 1893.

Sophora secundiflora f. *xanthosperma* Rehd. Journ. Arn. Arb. **10**: 134. 1929. TYPE: *L. W. Nuttall s.n.* Texas.

Shrub or small tree, to about 12 m. high; stipules minute or lacking; leaves 7-11-foliolate, the axis about 6-15 cm. long, sericeous, glabrescent, the lateral leaflets subopposite or alternate, the blades coriaceous, obovate to oblong, about 2-9 cm. long, 0.7-3.5 cm. broad, the apex obtuse, sometimes emarginate, the base obtuse or cuneate, the surfaces sericeous, often glabrate by maturity, the secondary venation reticulate, fairly prominent; bracts and bracteoles linear, the bracts to about 6 mm. long, the bracteoles shorter; flowers 20-30 mm. long, fragrant; calyx pallid-sericeous, 10-15 mm. long, the lobes deltoid, 3-5 mm. long, the tube hypanthoid, 7-10 mm. long; petals blue to violet-blue, the standard about one-third longer than the other petals; fruit coriaceous, sericeous, sometimes glabrescent, terete, usually torulose, 1-6-seeded, about 3-13 cm. long, (1-) 1.5-2 cm. in diameter at the seeds, the apex usually acuminate; seeds red (or yellow in f. *xanthosperma*), sublustrous, subellipsoid, about 10-17 mm. long, 10-15 mm. in diameter, the hilum orbicular to oblong, 2-4 mm. long and 1.5-2 mm. wide.

Distribution: Texas and New Mexico southward to Central Mexico.

MEXICO: CHIHUAHUA: Mouth of canyon 8 km. NW. of Cañon del Rayo, *Stewart 985* (GH).

COAHUILA: San Lorenzo Canyon, Saltillo, *Palmer 539* in 1905 (F, NY, UC, US). Chojo Grande, SE. of Saltillo, *Palmer 539 in* 1905 (GH), *721* in 1905 (A, F, GH, NY, UC, US). Sa. [de la] Paila, General Cepeda, *Hinton 16597* (NY, US). "De la Paila," *Rozynski 301* (NY). Sierra Pata Galana, *Purpus 1843* (BM, F, GH, UC, US). "S. Anahuac, Sta. Catarina," *Hinton 16933* (GH). Sierra Encarnación, *Nelson 3899* (NY, US). Sierra Mojada Mts., *Jones 169* (POM, US), *s.n.* (DS). San Lázaro, *Wynd & Mueller 136* (A, K, NY, US); *Mueller 3100* (GH, UC). "Cañon Espantosa," *Schroeder 49* (GH). Monclova, Sierra de Gloria, *Marsh 2003* (F, GH). Muzquiz, Sorpresa Spring, *Marsh 348* (F, GH, MEXU). La Esmeralda, *Juzepczuk 671* (F). San Antonio de los Alamos, *Johnston & Muller 938* (GH). Aguaje del Pajarito, N. of Puerto Colorado, *Johnston 8688* (GH). 4 km. W. de El Misterio, *Mendiola s.n* (ENCB). Sierra de la Madera, "La Cueva," Charretara Canyon, *Johnston 9115* (GH, MEXU). Canyon del Rayo, Sierra del Diablo, *Stewart 985* (GH). Cañon de Hidalgo, Sierra Mojada, *Stewart 1053* (GH). W. slopes of Sierra del Carmen, *Stewart 1689* (GH). Parrás, *Palmer 2133* in 1880 (K); *Aguirre 366* (MEXU).

NUEVO LEON: "New Leon," *Mexican Boundary Survey, Thurber s.n.* (F). Monterey, *Palmer 265* in 1880 (A, GH, K, NY, US); *Pringle 3071* [*3011?*] (A, ENCB, GH, MEXU), *10154* (BM, F, GH, K, MEXU, NY, UC, US); *Johnson & Barkley 16230 M* (F, GH); *Arsène* [*Bro. Abbon 245*] *6175* (A, US); *Mueller & Mueller 504* (MEXU); *White 1492* (GH); *Kenoyer 1105* (F). "Mts. 15 mi. W. of Icamole," *Safford 1265* (A, US). Between Cienequillas and Pablillo, *Mueller & Mueller 888* (A, F), *3602* (MEXU). Cerro Potosí, Galeana, *Schneider 1083* (F); *Edwards 46* (DS), *76* (F); *Mueller & Mueller* 518 (A). Near Doctor Arroyo, *Shreve & Tinkham 9387* (GH). Lampazos, *Edwards 310* (RSA), *414A* (F). Chipinque, Sn. Pedro Garza García, *Marroquin 696* (ENCB).

TAMAULIPAS: Between Victoria and Jaumave Valley, *Nelson 4443* (F, GH, US); *Rozynski 701* (F, NY). La Sardiña, *Bartlett 10957* (F, US). Cerro de los Armadillos, San José, *Bartlett 10388* (A, DS, GH). Sierra de San Lucas, *Rozynski 658* (CAS, F, K, NY, US). 9 mi. W. of Palmillas on road to Tula, *M. Johnston 5386* (MEXU).

DURANGO: Peñón de Covadonga, cerca de Yerbanís, Peñón Blanco, *Parey 3125* (ENCB).

ZACATECAS: Concepción del Oro, *Palmer 269* in 1904 (F, GH, K, NY, US); *Shreve 9369* (GH).

SAN LUIS POTOSÍ: San Luis Potosí, *Parry & Palmer 200* in 1878 (BM, F, GH, K, MICH, NY, US). Minas de San Rafael, *Purpus 5186* (BM, F, GH, MEXU, NY, UC, US). Charcas, *Lundell 5156* (A, F, MICH, UC). Amoles, *Graber 222* (US). Cedral, *Juzepczuk 413* (F). Mineral de Guadalcazar, *Villada 17* (MEXU). "Mt. Mitras," *Roybal 18* (UC). 10 km. W. of Guadalcazar, *Rzedowski 4924* (ENCB). Cañon E. of

Laguna Seca, Soledad, *Rzedowski 4234* (ENCB). Between Charco Blanco and Aguaje de Garcías, Guadalcazar, *Medellín 1561* (ENCB). 3 km. E. of Mineral de Catorce, *Rzedowski 7263* (ENCB, MICH). 3 km. E. of Corazones, Villa Hidalgo, *Rzedowski 8083* (ENCB, MICH).

QUERETERO: Pilón, *McVaugh 10362* (MEXU, MICH, US).

HIDALGO: Cardonal, *Ehrenberg s.n.* (US); *Moore 2166* (GH, UC). 4 km. NW. of Cardonal (El Mayorazgo), *González-Quintero 2514* (ENCB). Between Actopán and Ixmiquilpan, *Miranda 8996* (MEXU). Sierra de la Mesa, *Rose, Painter, & Rose 9094* (US). Km. 145, carretera México-Laredo, *Takaki s.n.* (ENCB). Cardonal, 18 km. NW. of Ixmiquilpan, *González-Quintero 2370* (ENCB). 3 km. S. of Santuario, Cardonal, *González-Quintero 2095* (ENCB).

Puebla: "Cerro de Matzize, near Oaxaca," *Purpus s.n.* (UC).

Local names: Colorín, chilicote, patiol, patol, frijolillo (Mexico); Texas mountain laurel, coral bean, mescal bean (United States).

The yellow-seeded form cited above is known from Texas and may or may not occur in Mexico.

In addition to the five species of *Sophora* native to Mexico, the Japanese Pagoda Tree, or Chinese Scholar Tree, *S. japonica* L. (*Styphnolobium japonicum* (L.) Schott) has been introduced in the valley of México. There are a number of trees in Chapultepec Park, in Mexico City, and a specimen, *Matuda* (no. *21189*) was collected "en ladera seca, Bosque de los pinos. Ajpsco, D. F." The trees of this species are fairly tall, to about 20 meters high, deciduous, with yellowish-white flowers about 10-15 mm. long, and glabrous, moniliform pods.

Three species of *Sophora* occurring in border states, *S. affinis* Torrey & Gray in Texas, *S. arizonica* S. Wats. and *S. formosa* Kearney & Peebles in Arizona, are as yet unknown in Mexico.

Tribe 2. PODALYRIEAE

Podalyrieae Benth. Enum. Pl. Hugel 27. 1839; Benth. & Hook. Gen. Pl. 1: 437. 1865. TYPE: *Podalyria* Lam.

Shrubs or perennial herbs; leaves commonly digitately 3-foliolate, sometimes pinnate, sometimes simple, 1-foliolate, or multifoliolate; stipules present or absent; inflorescences terminal or axillary, usually racemose, or the flowers sometimes solitary; corolla papilionaceous; petals free or the keel petals joined; calyx campanulate with 5 subequal lobes or teeth, the vexillar lobes sometimes connate, valvate or imbricate in bud; stamens 10, the filaments separate to the base, equal or alternately subequal in length, the anthers usually uniform, ellipsoid, dorsified; ovary 1-many-ovulate, the style glabrous or with a ring or hairs below the stigma; fruit 2-valved, commonly dehiscent; seed reniform or subreniform, the hilum lateral, subapical, sometimes carunculate.

Only *Pickeringia, Thermopsis,* and *Baptisia* are native to America. Only *Pickeringia* crosses the line into Mexico, in northern Baja California. *Thermopsis* is found in the United States south to the border states, Texas to California, and *Baptisia* occurs in Texas, but neither genus is known from Mexico.

8. Pickeringia Nuttall ex Torrey & Gray, Fl. N. Am. **1**: 388. 1840, nom. cons., non Nuttall 1834. TYPE: *P. montana* Nutt. in Torrey & Gray, California.
   Xylothermia Greene, Pittonia **2**: 188. 1891, nom. nov. for *Pickeringia* Nutt. 1840.
   Prickothamnus Nutt. ex Taubert in Engler & Prantl, Natürl. Pflanzenfam. **3**, Abt. **3**: 203. 1892, nomen in synon.

The genus is monotypic; hence, the description is that of the species.

1. **Pickeringia montana** Nutt. in Torrey & Gray, Fl. N. Am. **1**: 389. 1840. TYPE: *T. Nuttall s.n.*, "summits of mountains near Santa Barbara," California. Figure 3
   Xylothermia montana (Nutt.) Greene, Pittonia **2**: 188. 1891.
   Xylothermia montana subsp. *tomentosa* Abrams, Bull. Torrey Bot. Club **34**: 263. 1907. TYPE: *L. Abrams 3530*, "near El Nido, San Diego County," California.
   Pickeringia montana var. *tomentosa* (Abrams) I. Johnst., Contrib. Gray Herb. *n.s.* **68**: 84. 1923.

Shrub, to about 2 m. tall, erect or semiprostrate, with spinose branches; stipules not seen, apparently lacking; leaves alternate, digitately 3-foliolate or sometimes unifoliolate, essentially sessile, the

leaflets coriaceous, elliptic to obovate, 5-20 mm. long, 3-10 mm. broad, entire, the apex acute or obtuse, the base cuneate, the upper surface glabrous, nitid or sparsely appressed-pubescent to sericeous or tomentulose, the lower surface lighter in color, glabrous to sericeous or tomentose, the secondary venation inconspicuous, the terminal, or middle, leaflet sometimes with a slightly longer petiolule and larger blade than the laterals; inflorescences subterminal ["flowers solitary in the axils of the leaves at the extremity of the branches" fide Nuttall], sometimes apparently terminal, racemose, the axes moderately pubescent to densely argenteo-tomentose or sericeous; bracts and bracteoles linear, acicular, 2-4 mm. long; flowers 10-20 mm. long; calyx campanulate, valvate in bud, sparsely appressed-pubescent to tomentulose, 5-7 mm. long, the teeth deltoid, 1 mm. long or less; petals free, reddish-purple or, rarely, whitish; stamens alternately subequal in length, about 10-15 mm. long, the anthers ellipsoidal, about 1 mm. long; ovary pallid-tomentose, commonly 6-10-ovulate, the style glabrous, the stigma terminal, minutely capitate-penicillate; fruit dehiscent, coriaceous, light brown, puberulent, linear, compressed, 1-10-seeded, about 2-5 cm. long, 4-5 mm. broad, and 2 mm. thick; seeds reniform, sublustrous, brownish-black, 3-4 mm. long, 2 mm. broad, and 1 mm. thick, the hilum minute, subapical.

Distribution: In chaparral, north central California to northern Baja California.

MEXICO: BAJA CALIFORNIA NORTE: Descanso Valley, *Moran 8427* (SD, US).

Local names: Chaparral pea, pea chaparral, stingaree bush (California).

The vesture of the plants is so variable and with so much intergradation it does not seem desirable to recognize a tomentose variety unless other degrees of pubescence are given equal consideration. The vegetative parts of the one collection thus far known from México are silvery sericeous.

SMITHSONIAN INSTITUTION
WASHINGTON, D. C. 20560

EVIDENCE FOR THE HYBRID ORIGIN OF PETASITES WARRENII AND P. VITIFOLIUS

ALFRED L. BOGLE*

The purpose of this paper is to present evidence for the hybrid origin of *Petasites warrenii* St. John, an endemic to the State of Washington. This interpretation is based on the study of herbarium specimens, on observations in the field of reproductive biology and distribution, and on the progeny from artificial hybridizations involving *P. warrenii* and its putative parents, *P. frigidus* var. *palmatus* (Ait.) Cronq. and *P. sagittatus* (Pursh) Gray. A portion of the evidence also suggests that *P. vitifolius* Greene, which has a much wider distribution across North America, is a product of the same hybridization complex which has produced *P. warrenii.*

TAXONOMIC HISTORY

The circumboreal genus *Petasites* Mill. (Compositae-Senecioneae) is represented in North America by four ill-defined native taxa, and two introduced species which have escaped from cultivation (*P. japonicus* Maxim., and *P. hybridus* (L.) Gaertn., Mey. & Sherb.). The systematics of the indigenous members is based almost entirely on leaf shape, and was last revised by Cronquist (1946, 1953). As a result of his revision the numerous species described from this continent up to that time (cf. Rydberg 1927) were reduced to only two, *P. sagittatus* (Pursh) Gray (Fig. 1B), and the polymorphic *P. frigidus* (L.) Fries, with three varieties: var. *frigidus* (Fig. 1K, L), var. *nivalis* (Greene) Cronq. (Fig. 1H, J), and var. *palmatus* (Ait.) Cronq. (Fig. 1A). The following key to the species and varieties is taken from those of Cronquist (1953, varieties of *P. frigidus*; 1955, *P. sagittatus.*)

1. Leaves evidently lobed, varying to coarsely few-toothed with 5-15 teeth on each side. .... *P. frigidus*

*Present address: The Arnold Arboretum, Harvard University, Cambridge, Massachusetts 02138

2. Leaves merely coarsely toothed or very shallowly and obscurely lobed: circumboreal, characteristically arctic, extending south, uncommonly, to central Washington. .... var. *frigidus*
2. Leaves evidently lobed.
   3. Leaves palmately or more often pinnipalmately lobed and veined, the lobes ordinarily not extending more than halfway to the base (or often deeper in western specimens, which are distinctly pinnipalmate); leaves seldom more than 2 dm. wide, seldom evidently wider than long; characteristically subarctic or of boreal forests, extending south to the Gaspé Peninsula of Quebec, northern Minnesota, and at high elevations in the mountains to northern Quebec. .... var. *nivalis*
   3. Leaves palmately lobed and veined, the lobes commonly extending well over half way to the base (or in western specimens often only about half way to the base); leaves tending to be broader than long, often very large (up to 4 dm. wide); more southern than the other varieties, extending south to California, Minnesota, Michigan, and Massachusetts. .... var. *palmatus*

1. Leaves varying from merely a little wavy and callous-denticulate to more commonly conspicuously dentate with 20 to 45 teeth on each side. Wet places: Alaska to Labrador, south to northeastern Washington, northern Idaho, Montana to Colorado, northern Minnesota and Wisconsin. .... *P. sagittatus*

This system was not without precedent. Hooker (1833) first suggested that the North American taxa might best be considered as varieties of a single species. Under the generic name of *Nardosmia* Cass. he recognized four distinct species (*N. frigida* Hook., *N. corymbosa* Hook., *N. palmata* Hook., and *N. sagittata* Hook.), but noted that they "are distinguished by very slight characters, and the numerous specimens before me, would, in the varied form of the foliage, lead to the suspicion that they in reality constitute but one species."

Herder (1865) reduced *Nardosmia palmata* and *N. corymbosa* to varietal status under *N. frigida*, but his revision went unheeded by North American taxonomists, who subsequently described several minor morphological variants as distinct species.

Rydberg (1927, pp. 310-315) recognized eleven distinct species, and in the fifteen years following his publication at least two new species and one variety were described.

It was to Herder's system that Cronquist especially referred in again revising the taxonomy of the group. The interested reader may consult his papers (1946, 1953, 1955) for comments and synonymy. This classification is now found in several major floristic works published within the past dozen years, and its nomenclature is followed here. It has been rejected by Hultén (1950, p. 1583), however, and is not followed by such authors as Anderson (1959), Moss (1960), and Polunin (1959).

Cronquist (1946) tentatively placed *Petasites warrenii* (Fig. 1D) in synonymy under var. *frigidus*, and later (1955) stated that in leaf form it was "approaching var. *nivalis*. Perhaps eventually to be recognized as a distinct variety." He also (1946) reduced *P. vitifolius* Greene (Fig. 1E, G; incl. *P. trigonophyllus* Greene) to synonymy under var. *nivalis*.

The peculiarities of form and distribution of *Petasites warrenii* prompted this investigation of the taxon, and of the possibility of interspecific relationships between *P. frigidus* var. *palmatus* and *P. sagittatus*.

MATERIALS AND METHODS

In the course of this study more than 1000 herbarium specimens of the North American taxa were examined. Those specimens which are considered to have originated in the complex of hybridization described here are listed below under a separate heading.

In the field the limits of distribution of *Petasites warrenii* were ascertained, and observations made on the nature of its inflorescences and reproduction. Live female plants of *P. warrenii* and *P. sagittatus* were transferred from the field to cultivation in the greenhouse for later use in artificial pollinations.

Artificial pollinations were made both in the field and in the greenhouse in the spring of 1960. In the greenhouse pollen from male plants of *Petasites frigidus* var. *palmatus* growing on the road embankment of U. S. 10, about one mile east of Issaquah, Washington, was transferred to flowers of female plants of both *P. sagittatus*, collected near Bona-

parte Lake, Okanogan Co., Washington, and *P. warrenii*, collected near Liberty, Kittitas Co., Washington. Pollinations were made and plants kept in insect-proof cages.

In the field, female flowers of *Petasites warrenii*, blooming near Liberty, were pollinated by flowers of male inflorescenses of *P. frigidus* var. *palmatus* blooming near the summit of Snoqualmie Pass, Washington (a linear distance from Liberty of approximately forty miles). The pollinated inflorescences were protected from insects by covering the scapes with a nylon stocking, the lower, open end of which was tied shut around the scape and supporting wire frame.

Pollen was applied to the protruding styles of as many flowers and heads as possible. It could not be determined which styles were in a receptive condition, or how many received pollen. In both locations adjacent flowering inflorescences were left unpollinated as a simple test for natural pollination. Unfortunately, male plants of *Petasites sagittatus* were not available for making reciprocal crosses, and male plants of *P. warrenii* are unknown.

OBSERVATIONS AND RESULTS

Reproductive biology

All of the North American *Petasites* are polygamodioecious, rhizomatous, herbaceous perennials, utilizing both sexual and asexual modes of reproduction. Proliferation by means of bracteate rhizomes is predominant. In this way large clones develop from a single vegetative fragment or seedling.

Inflorescences of *Petasites* are variously described as polygamodioecious, subdioecious, or dioecious. All heads examined by the writer of the taxa concerned here have contained both bisexual disc florets and unisexual pistillate ray florets in varying numbers. Field observations, however, indicate that the plants are functionally dioecious, and are here termed male and female. Heads of the functionally male scapes contain numerous (up to about 60 in var. *palmatus* of Washington) perfect, tubular, disc florets surrounded by a single peripheral row of sterile, pistillate, ray florets. The anthers of the disc florets are the sole source

of viable pollen; their ovaries are sterile. In contrast, heads of functionally female inflorescences contain at their centers only a few (1-5) reduced, perfect but sterile, disc florets. These are surrounded by many (up to about 200 in var. *palmatus* of Washington) fertile, pistillate, ray florets. Seed is formed only in the female inflorescences.

Considering the essentially dioecious nature of the plants and the predominance of vegetative reproduction, it is not unusual to find large colonies or clones which are entirely of one sex or the other. It appears significant, therefore, that extensive searching through the colonies of *Petasites warrenii* over a period of two years has shown that all plants of the taxon are female. This observation also applies to all of the herbarium specimens examined. In addition, innumerable inflorescences were checked at maturity for seed development, but none was found; this suggests the absence of a male pollen parent and of agamospermy.

When both types of inflorescence occur in proximity, pollination, effected by a variety of insects (including butterflies, hoverflies, humble-bees, honey-bees, and beetles on var. *palmatus* in the Puget Sound region), usually takes place and the sexual cycle is completed.

Once the pollen has been shed the male inflorescences quickly wilt and die, while the female inflorescences persist, undergoing considerable increase in height. At maturity the involucral bracts of the fruiting heads reflex, allowing the crowded pappus filaments of the many flowers to expand into a conspicuous, cottony mass. The seeds are carried away on the wind, or fall to the ground.

In the Puget Sound region seeds of var. *palmatus* have been observed to germinate while still attached to the receptacle, while in the laboratory fresh seed will ordinarily germinate on moist filter paper within 24 hours. The period of viability appears to be rather short, however, perhaps as little as a few weeks in duration.

Somatic chromosome counts by Kruckeberg (Ornduff et al. 1943) on plants from the Pacific Northwest indicate that x = 30 for *Petasites warrenii, P. sagittatus,* and *P. frigidus* var. *palmatus (P. speciosus).* Søensen and Christiansen

(1964), however, report counts of $2n$ = approx. 60 for *P. sagittatus* ($2n$ = 58, 59, 60), and *P. frigidus* var. *palmatus* ($2n$ = 60, 61, 62), in plants from Fort Chimo, Labrador. The latter authors suggest that the basic chromosome number in the genus *Petasites* is 29, with "A few small chromosomes, presumably B-chromosomes" accounting for the varying numbers in these and other species of the genus.

Herbarium studies

Among herbarium specimens the leaf form of *Petasites warrenii* (Fig. 1D) can be matched by some specimens among the wide variety of forms once relegated to *P. vitifolius* (Fig. 1E, G), but now included with *P. frigidus* var. *nivalis* (Fig. 1H, J). In some instances the varying specimens labeled *P. vitifolius* have been collected in areas where *P. frigidus* var. *palmatus* (Fig. 1A) and *P. sagittatus* (Fig. 1B) are sympatric and growing in close proximity, as is apparent in the collections of Porsild and Breitung along the Canol Road in Yukon Territory, in the collections of McCalla in the vicinity of Banff, Alberta, or in specimens collected by the writer and others on the shores of Lake Itasca, Clearwater Co., Minnesota.

The ranges of the taxa primarily concerned in this pattern of hybridization, as determined from the label data of herbarium specimens and from the writer's observations in the field, are discussed below. Their general distribution in the Pacific Northwest is illustrated in Fig. 4.

Petasites frigidus var. *palmatus* (Ait.) Cronq. (Fig. 1A) spans the North American continent. It ranges from Newfoundland south to New York, and westward through the border provinces of Canada and the northern portions of Michigan, Wisconsin, and Minnesota, to Vancouver Island, British Columbia. In the continental interior it extends northward to southeastern Yukon, and to the arctic coast of the Northwest Territories, where the segregate species *P. arcticus* Porsild (Porsild 1943, p. 74) has been described on the basis of collections of var. *palmatus* from the Mackenzie River delta area. On the west coast a robust ecotype, formerly designated *P. speciosus* (Nutt.) Piper,

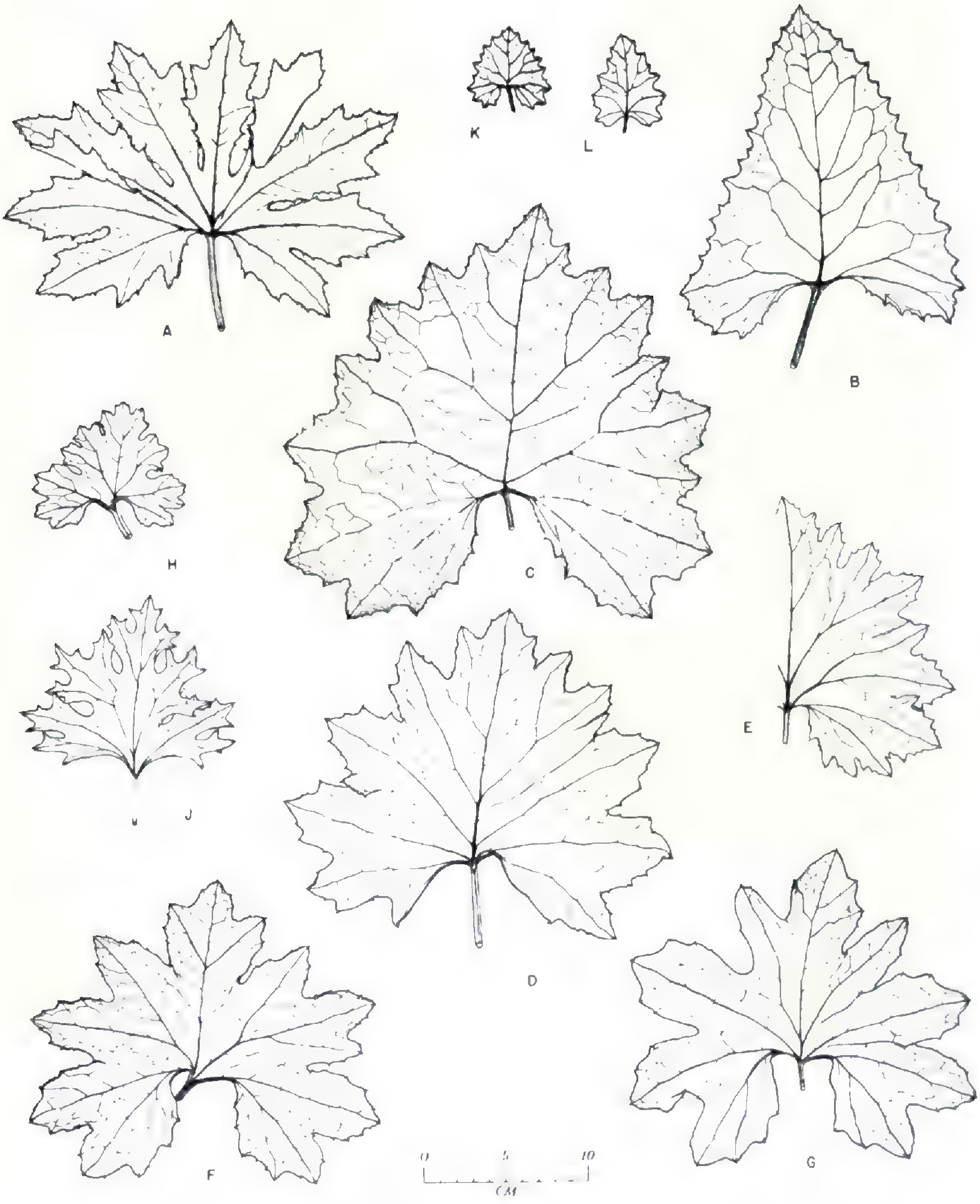

Figure 1. **A.** *Petasites frigidus* var. *palmatus (P. speciosus),* **B.** *P. sagittatus,* **C.-G.** various forms of the hybrid *P.* × *vitifolius.* **C.** *P. sagittatus* × *frigidus* var. *palmatus,* **D.** *P. warrenii,* **E.** *P. vitifolius,* McCalla 9367. Vermillion Lake, Banff, Alberta, (labeled *P. palmatus*), **F.** *P. warrenii* × *frigidus* var. *palmatus,* **G.** *P. vitifolius* Itasca State Park, Minnesota, **H.** *P. frigidus* var. *nivalis* Mt. Rainier National Park, Washington, **J.** *P. frigidus* var. *nivalis* Mt. Garibaldi, Garibaldi Provincial Park, British Columbia, **K.** *P. frigidus* var. *frigidus,* Coll: Montell Lappland (Finland), **L.** *P. frigidus* var. *frigidus,* Spetzman 873. Alaska, Arctic slope.

inhabits the cool, moist, western slopes of the Cascade and Coast ranges to altitudes of about 2500 feet, and ecologically favorable places in the valleys of the foothills on the east side of the Cascades in Washington and Oregon (Fig. 4). The variety also has a far-eastern distribution in Sakhalin (Sugawara 1940), where the segregate species *P. tatewakianus* Kita. has been designated (Kitamura 1940), and the natural hybrid *P. japonicus* subsp. *giganteus* × *P. tatewakianus* Kita. described (Kitamura 1942, p. 165).

Plants of var. *palmatus* thrive in the moist soils or wet clays of disturbed sites such as stream banks, road cuts and embankments, or logging roads in the Pacific Northwest, and in the moist soils of the forest floor in Minnesota.

The range of *Petasites sagittatus* (Pursh) Gray (Fig. 1B) extends from Labrador westward through Canada to British Columbia, Yukon, and on into Alaska (see map no. 322 in Porsild 1957). It occurs in northeastern Washington (Fig. 4), northern Minnesota, and southward sporadically in the Rockies from Idaho and eastern Montana to southern Colorado. A large portion of its range overlaps that of var. *palmatus*, and in some places they may be found growing in close proximity.

Plants of the species observed by the writer in Washington, Colorado, and Minnesota have invariably been growing in shallow standing water or marshy situations, with their rhizomes buried to a depth of several inches in the soft mud.

The first collection of *Petasites warrenii* St. John (Fig. 1D) was made by F. A. Warren in 1926 along Swauk Creek, near the town of Liberty, in the Wenatchee Mountains of Kittitas County, Washington (Fig. 2, 4). Field work in the area has revealed its distribution to be restricted to the moist or wet soils of stream banks, or soft muds of marshy alluvial flats along the courses of three streams: the Boulder, Williams, and Swauk creeks (Fig. 2). Boulder Creek drains into Williams Creek, which flows through the old goldminers' town of Liberty and empties into Swauk Creek. The scattered colonies of *P. warrenii* found along Swauk Creek and lower Williams Creek have probably

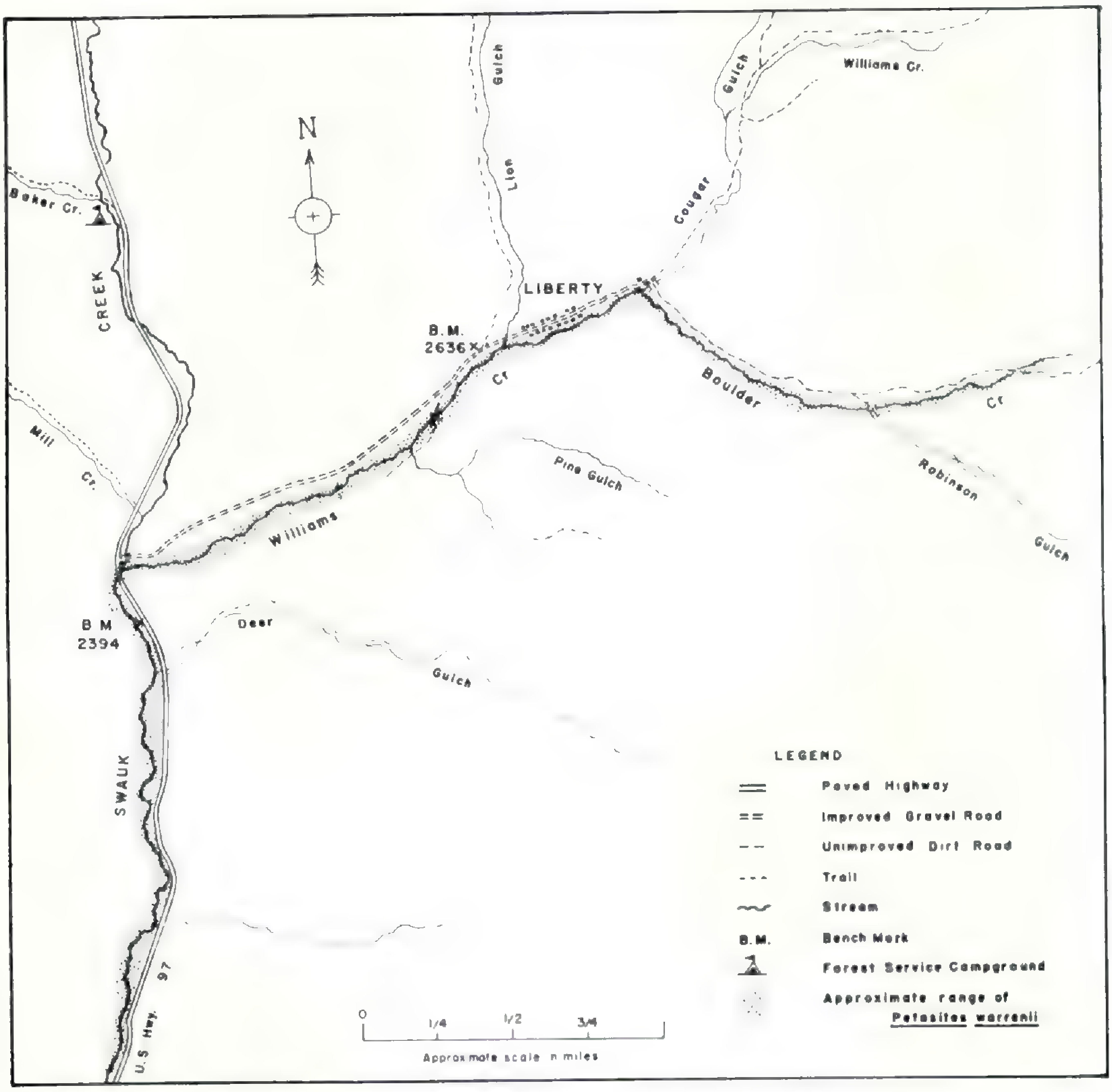

Figure 2. Distribution of *P. warrenii* = *P.* × *vitifolius* in area of Liberty, Kittitas Co., Washington.

developed clonally from fragments of rhizome washed downstream from the areas of most extensive development along Boulder Creek. The linear distance of distribution along the three streams is roughly six miles.

Occasional plants of *Petasites frigidus* var. *palmatus* are found in ecologically favorable situations along these streams, and one pistillate clone has been observed growing within a large colony of *P. warrenii*. These scattered plants probably arise from seeds carried across the mountains on the wind from the main area of distribution on the west side of the Cascades.

Petasites vitifolius Greene (Fig. 1E, G) is known from lower elevations in British Columbia and Alberta, and eastward to northern Minnesota and the Gaspé Peninsula of Quebec. This distribution covers essentially that portion of the continent in which the ranges of var. *palmatus* and *P. sagittatus* coincide. Plants of the taxon utilize the habitats of either putative parent, but do best in the marshy conditions typical of *P. sagittatus.*

Results of artificial hybridizations.

Seed production in plants artificially pollinated in the field was low. Thirty-seven apparently viable seeds were recovered from inflorescences of *Petasites warrenii.* Results were considerably better in the greenhouse, where 458 apparently good seeds were taken from *P. warrenii* heads, and 111 from heads of *P. sagittatus.* Fruits containing viable seeds can be recognized by their larger size, turgid condition, and light- to dark-brown color. Ovaries in which embryos fail to develop are small, withered, and lack color. In addition, seed development is accompanied by a considerable elongation of the pappus. Visual inspection is sufficient for separation.

Some of the hybrid seed obtained was immediately germinated, and mature plants have since developed and flowered in the greenhouse. These hybrids may be tentatively designated as *Petasites sagittatus* × *frigidus* var. *palmatus,* and *P. warrenii* × *frigidus* var. *palmatus.* They are discussed briefly below, and the forms of their leaves and style branches are compared with those of the parents in figures 1 and 3 respectively.

Petasites sagittatus × *frigidus* var. *palmatus.* (Fig. 1C).

Mature leaves of this F_1 hybrid are shallowly lobed, with the lobes entire to sinuate-dentate, or again shallowly lobed. In Fig. 1 the general leaf form of this hybrid (Fig. 1C) is compared with those of the other North American taxa, including: *Petasites warrenii* (Fig. 1D) ; a leaf representative of collections, variously labeled *P. vitifolius* or *P. palm-*

atus, made by McCalla in the vicinity of Banff, Alberta (Fig. 1E); two specimens of *P. frigidus* var. *frigidus* (Fig. 1K, L), to which *P. warrenii* is attributed; and two leaves of *P. frigidus* var. *nivalis* (Fig. 1H, J), to which the various forms of *P. vitifolius* are attributed.

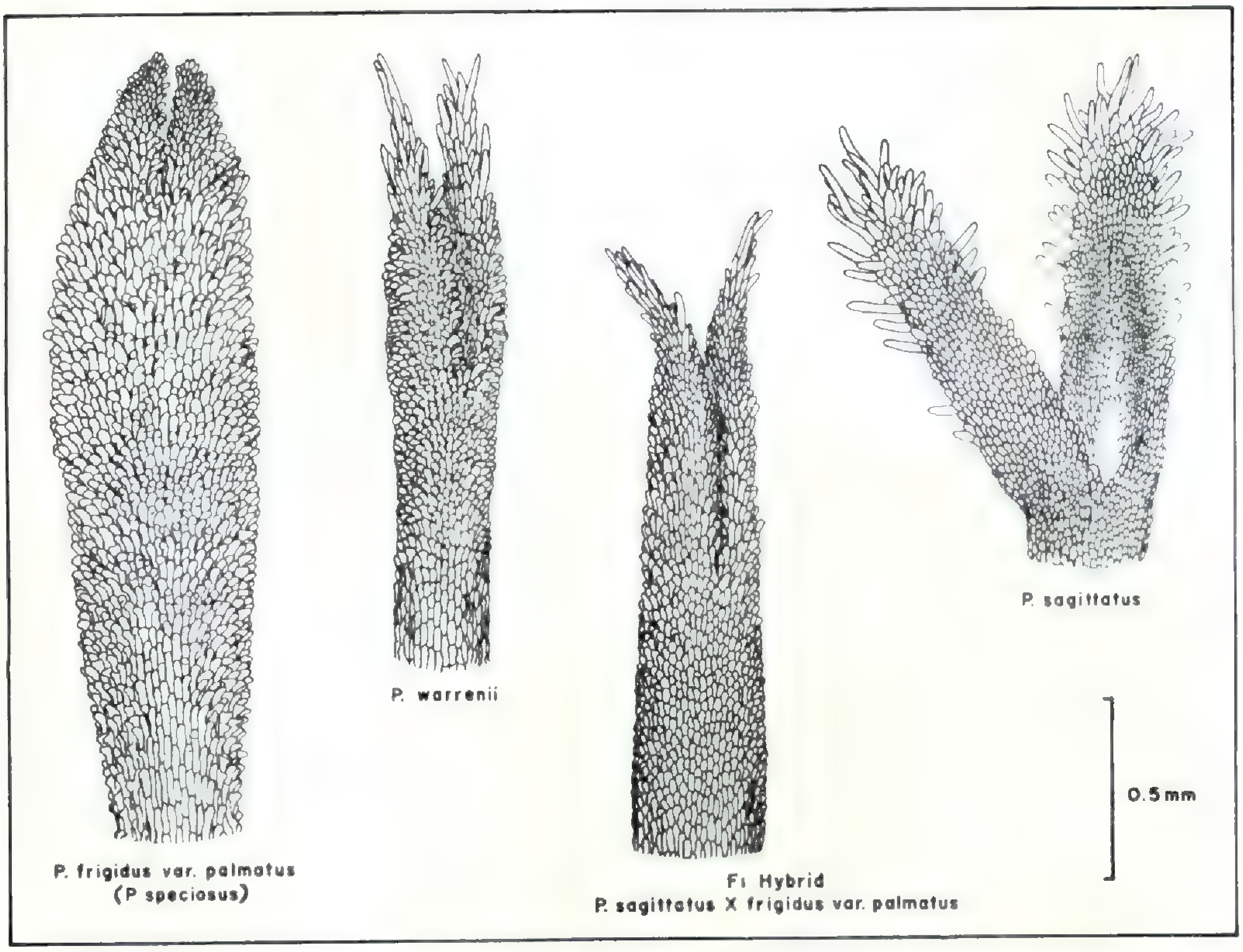

Figure 3. Comparison of the style branches of parent and hybrid forms.

The style branches of the parental taxa, the artificial F_1 hybrid, and *Petasites warrenii* are compared in Fig. 3. The styles of *P. frigidus* var. *palmatus (P. speciosus)* are clavate, with a very shallow notch about 0.5 mm deep at the tip. The surface of the entire style tip is papillose, with no elongated setae. The styles of *P. sagittatus* bear more or less oblong branches which are about 1.0-1.5 mm long, with long sweeping hairs clothing the margins and tips. In *P. warrenii*, and *P. sagittatus* × *frigidus* var. *palmatus*, the style branches are more or less intermediate in length, and terminate in elongate hairs very similar to those in *P. sagittatus*, but their margins are merely papillose. The style

branches of both the artificial and supposed natural hybrids thus compare favorably in form, and are intermediate between those of the parental taxa. Although the styles illustrated here were taken from the somewhat reduced, sterile, disc florets of the female heads of the four taxa, comparison with their larger, fertile counterparts in the male heads (with the exception of *P. warrenii*) shows their form to be representative.

The form of the bracts of the inflorescence scape, the margins of the involucral phyllaries, and of the flags of the anther connectives (although not illustrated here) also compare favorably among the artificial and supposed natural hybrids, and are intermediate between those of the parent taxa (cf. illustrations in Bogle 1961).

Petasites warrenii × *frigidus* var. *palmatus*. (Fig. 1F).

If, on the basis of the foregoing morphological evidence, a hybrid origin similar to the above can be accepted for *Petasites warrenii*, then the combination *P. warrenii* × *frigidus* var. *palmatus* is the equivalent of a backcross of an F_1 hybrid to the palmate parent. Leaf form among progeny of *P. warrenii* × *frigidus* var. *palmatus* does not exhibit the relative uniformity seen in offspring of *P. sagittatus* × *frigidus* var. *palmatus*, and the lobing is deeper than that of the F_1 hybrids. It was found that the various forms recovered among the backcross progeny compare favorably with many of the variations of *P. vitifolius* found in nature. The mature leaf form of one of these hybrids (Fig. 1F) is compared with that of a collection of *P. vitifolius* from Itasca State Park, Minnesota (Fig. 1G), and with leaves of *P. frigidus* var. *nivalis* of alpine habitats in the Cascade mountains of Washington and British Columbia (Figs. 1H, J), the variety to which *P. vitifolius* has been subordinated.

Pollen viability

Pollen grains from available male plants were stained in lactophenol-aniline blue to obtain a rough measure of pollen viability. Two to four flowers from each inflorescence were

tested, and a minimum of 200 grains were counted for each flower. The number of plants tested is indicated in parentheses after each binomial. The ranges of stainability percentages found are as follows:

P. frigidus var. *palmatus (P. speciosus)*, (3)	95-99%
P. sagittatus × *frigidus* var. *palmatus*, (10)	29-99
P. warrenii × *frigidus* var. *palmatus*, (3)	29-44
P. vitifolius, (1)	45-63

Although the range of stainability is rather wide in *Petasites sagittatus* × *frigidus* var. *palmatus*, more than half of the counts obtained are in excess of sixty percent. Viability may vary considerably from flower to flower within an inflorescence, but in most cases the extremes of range are from different plants rather than from flowers of the same plant. Increased complexity of the genome, as in *P. warrenii* × *frigidus* var. *palmatus*, appears to be accompanied not only by reduced pollen viability, but by increased variability in the size of pollen grains and in the stainability of their protoplasts; it thus becomes increasingly difficult to distinguish between viable and inviable grains.

DISCUSSION

The opinions of Hooker, Herder, and Cronquist reflect the impression given by herbarium specimens that the three morphological "peaks" of leaf form embodied in the varieties of *Petasites frigidus* (Fig. 1) are almost completely intergrading. Hooker (1833) maintained *P. sagittatus* as a species, while suggesting that it, too, intergrades with the other forms. Cronquist considers *P. sagittatus* sufficiently distinct to be maintained as a separate species. The evidence presented above, however, suggests that *P. warrenii*, and many of the variants formerly lumped in *P. vitifolius* but now assigned to *P. frigidus* var. *nivalis*, are actually manifestations of hybridization between *P. sagittatus* and *P. frigidus* var. *palmatus*.

Many of the various leaf forms of putative hybrid origin found in nature can be matched by similar forms found among the artificially created hybrid progeny. The morphological intermediacy seen in the leaves and style

branches of *Petasites warrenii* and the artificial F_1 hybrids is also apparent in their inflorescence bracts, phyllaries, and anther connectives. Such intergradation of form could doubtless be demonstrated in other areas of the continent where hybrids are being formed, but the F_1 hybrids should be expected to reflect the morphological variation seen in the parent taxa from different geographical areas. The deeper, narrower lobing of midwestern representatives of var. *palmatus*, for example, may result in deeper lobing in F_1 hybrids than that apparent in *P. warrenii* and the artificial F_1 hybrid illustrated here, both of which reflect the broader, more shallowly lobed west coast phase of var. *palmatus* (i.e., *P. speciosus*).

Pollen stainability percentages indicate high fertility, or at least some fertility, in plants of both the F_1 and more complex hybrid generations. Such fertility in nature has probably enhanced the variation among hybrids through

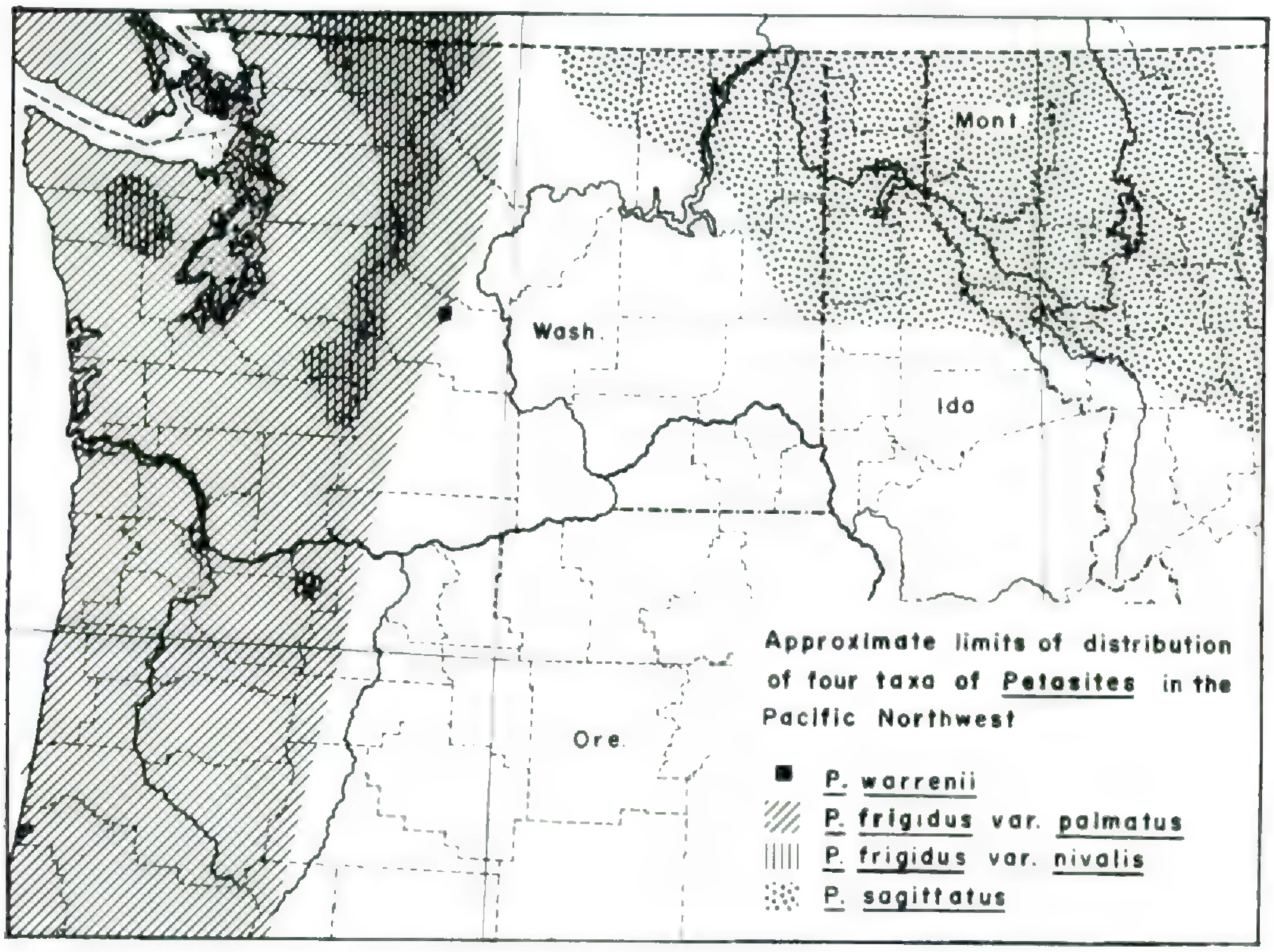

Figure 4. Approximate limits of distribution of four taxa of *Petasites* in the Pacific Northwest.

the formation of F_2 and F_3 combinations, and backcrossing of these to the parent stocks.

It is now necessary to remove the taxa of hybrid origin from synonymy under the varieties of *Petasites frigidus*, and to consider the position of *P. sagittatus*. Removal of *P. warrenii* from var. *frigidus* eliminates the variety from the State of Washington, restricting the southern limit of its range to northern British Columbia. Transfer of *P. vitifolius* from var. *nivalis*, however, shrinks the transcontinental range of the variety to a much smaller arctic-alpine distribution in northwestern North America, where it then consists only of the former species *P. nivalis* Greene (Fig. 4) and *P. hyperboreus* Rydb. Even with *P. vitifolius* removed var. *nivalis* remains a polymorphic group of unknown origin, possibly arising in hybridization between *P. frigidus* var. *frigidus* and var. *palmatus*, as suggested by Hultén (1950, p. 1583).

With regard to the position of *Petasites sagittatus* it could be argued that there is now a basis for reducing the species to varietal status within the *P. frigidus* complex if genetic compatibility and interspecific hybridization are to be the criteria for classification. Hultén (1950, p. 1583), however, does not agree with the idea of uniting such diverse forms under a single specific epithet. He would prefer to maintain the varieties as distinct species and recognize the hybrids under formula designations. The latter is the course preferred by the writer in the case of *P. sagittatus*. The link of hybridization between *P. sagittatus* and *P. frigidus* var. *palmatus* is strong. On the basis of four collections from widely scattered points in Alaska and Yukon, Hultén has also proposed hybridization between *P. sagittatus* and *P. frigidus* var. *frigidus* (see map 1177c, Hultén 1950). But in neither case of hybridization is the characteristic form of *P. sagittatus* "swamped" by the hybrid intermediates.

On the basis of herbarium studies the areas of primary hybridization to the south, at least, appear to be few. The number of probable F_1 specimens similar to those illustrated here is also few compared with the number representing

apparently more complex hybrid combinations such as *Petasites warrenii* × *frigidus* var. *palmatus*. Wide dispersal of wind borne hybrid seed may magnify the extent of actual primary hybridization between the parent species, while persistence of hybrid plants through vegetative reproduction may greatly increase the period of time, as well as the number of individuals, available for further hybridization. *P. warrenii* is a case in point. Its exact origins are unknown. It may have developed from a chance hybrid seed blown in from some area to the north where the putative parents are hybridizing, or it may have arisen through hybridization in the Swauk valley if *P. sagittatus* occurred there in the past. Occasional female plants of var. *palmatus* have been found among the colonies of *P. warrenii*. Should a male plant of var. *palmatus* become established among the strictly female clones of *P. warrenii* a new phase of hybridization could begin.

In the southern portions of their ranges *Petasites sagittatus* and *P. frigidus* var. *palmatus* are distinct morphologically and ecologically, and their hybrid offspring are recognizable. The writer feels that extensive field work and detailed study in critical northern areas, to delimit more precisely the varieties and their inter-relationships, should precede expansion of the *P. frigidus* complex to include *P. sagittatus*.

CONCLUSIONS

Petasites warrenii and *P. vitifolius* (including *P. trigonophyllus*) are merely phases of a large and very variable group originating in hybridization between *P. sagittatus* and *P. frigidus* var. *palmatus*. Repeated interbreeding among hybrids, and backcrossing to the parent stocks, has probably occurred, producing the wide range of variability now seen among the hybrids. The following hybrid designation is proposed to include the intermediate forms:

Petasites × *vitifolius* Greene (pro sp.) = *P. sagittatus* × *P. frigidus* var. *palmatus*.

P. warrenii St. John, Res. Stud. State Coll. Wash. 1:109. 1929.

P. vitifolia Greene, Leafl. 1:180. 1906.

P. trigonophylla Greene, Leafl. 1:180. 1906.

Listed below are the herbarium specimens examined during this investigation which are considered to be of hybrid origin. The specimens of all taxa examined and annotated are listed in a previous paper (Bogle 1961). Abbreviations used to designate herbaria are those proposed by Lanjouw and Stafleu (1959). Specimens of the artificial hybrids synthesized during this study are on deposit in the herbaria of the University of Washington, the University of Minnesota, and the Gray Herbarium of Harvard University.

Abbe, Abbe, & Marr 3221 (MIN, US); *Ahlgren 1032* (MIN); *Anderson, J. P. 10414* (ISC); *Anderson, J. R.* (WSU *44648*); *Becket M-55-23* (MIN); *Breitung 1794, 15862* (UAC); *Brinkman 4254* (US); *Brown 45* (ISC); *Butters, Huff, & Rosendahl 2755* (MIN); *Campbell 150, 569* (CAN); *Eastham* (UBC *11922a, 11922b*); *Eastwood 476* (CAN, WS), *481* (US, WS); *Fernald & Collins 259* (MIN, US); *Fernald, Griscom, & Mackenzie 26080* (US); *Garton 1455* (US), *2641, 8530* (MIN); *Gillet 2315* (US); *Harper 3078* (MIN); *Hitchcock & Marsh 3283* (WTU, WS); *Krivda 1861* (UBC); *Lakela 1137a* (MIN, US), *8081, 8252, 11633, 12882, 18258, 20587* (MIN); *Lewis 306* (US); *Macoun* 6/10/1880 [TYPE of *P. vitifolius*] (US), (WSU *46231*); *Marie-Victorin & Rolland-Germain 27567* (US); *Marie-Victorin, Rolland-Germain, & Louis-Marie 21232* (US); *McCalla 2059a, 3704, 7061, 11310* (UAC), *9192, 9235, 9275, 9284, 9367, 9560, 9580* (UBC); *Moir 812, 947, 1107, 1435, 2010, 2040* (MIN); *Moore & Moore 11028* (MIN); *Moss 2006, 2355, 4219, 4264, 8846* (UAC); *Moyle 948, 1091* (MIN); *Nelson 2426* (MIN); *Ownbey 3216* (MIN); *Porsild & Breitung 9342, 9424* (CAN), *9759* (WTU), *10333* (CAN, ISC), *10334* (ISC), *11733* (US); *Richards 4763* (MIN); *Richardson 14678* (CAN); *Rosendahl 4752* (MIN); *Rosendahl & Moyle 2218* (MIN); *Sandberg 155a* [TYPE of *P. trigonophyllus*] (US, WS), (US *45059*), (MIN 212577); *Scoggan 5141, 5667* (UAC); *St. John, English, Jones, & Mullen 8106* (WS); *Taylor & Lewis 392* (UBC); *Thompson 5961, 8204* (WTU), *11310* (MONTU, WS, WTU), *14503* (ID, MIN, UAC, UBC, WS); *Tisdale* (UBC 8736); *Turner 1725, 4367, 4514* (UBC), *4364, 4367, 4406, 4413* (UAC); *Warren 380, 542* [TYPE of *P. warrenii*], *809* (WS).

ACKNOWLEDGEMENTS

The writer wishes to express sincere thanks to Dr. A. R. Kruckeberg, at whose suggestion and under whose guidance this work was begun. I am also indebted to the Society of Sigma Xi for a Grant-in-Aid of Research which has made

possible herbarium studies and field collections both in Minnesota and abroad. The Department of Botany of the University of Minnesota has allowed the use of its greenhouse and herbarium facilities for the continuation of this study. Dr. Kruckeberg, Dr. E. C. Abbe, Dr. G. B. Ownbey, and Dr. T. Morley very kindly criticized earlier drafts of this paper. Finally, I would like to express my gratitude to the curators of the following herbaria for the use of specimens essential to this study: University of Alberta, University of British Columbia, National Museum of Canada, University of Idaho, Iowa State University, University of Minnesota, Montana State University, United States National Museum, University of Washington, and Washington State University.

DEPARTMENT OF BOTANY
UNIVERSITY OF WASHINGTON, SEATTLE

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BIOMETRIC AND TAXONOMIC USES OF CELLULOSE ACETATE PLASTIC

Edward E. Terrell

Plastics have been used in botany as embedding media and as films, sheets, or bags to hold or cover specimens. The present paper discusses one particular kind of plastic, cellulose acetate, and its versatility and usefulness in taxonomy.

The late Prof. N. C. Fassett described (1951, pp. 141-2) his method of mounting small seeds of species of *Callitriche* on transparent 1″ by 1½″ cellulose acetate slides. These mounts were easy to handle, permanent, and storable in the envelopes attached to herbarium sheets. To attach seeds to slides Fassett used acetone in which pieces of the cellulose acetate plastic were dissolved. This quick-drying solution also was used to reattach plants to herbarium sheets. Slides were labelled with india ink. Fassett (1949) used slender slivers of the plastic as aids in picking up seeds and other tiny objects by static electricity.

The most valuable characteristic of the plastic is its transparency. Inscriptions made on its surface or plant parts mounted on it may be superimposed on plant material, permitting a side-by-side comparison through a dissecting microscope or hand lens. Two other characteristics of the plastic are also important: it may be cut in any size or shape with a paper cutter or shears; its surface may be easily inscribed with lines, numerals, or other markings. Conventional glass slides do not have the latter advantages.

Plastic slides prepared in 1961 appear permanent. Clear nail lacquer ("fingernail polish") was used as a glue — it is inexpensive, quick-setting, and has its own applicator brush. Slides (Fig. 1) have been made in two sizes: 3″ by 1″ for storage in standard microscope slide boxes; and 6¼″ by 1″ for storage in double-rowed wooden slide boxes by removing the wooden center partition. The longer slides are more useful for holding long, narrow plant parts, e.g., grass spikes, leaves, or portions of stems. Both sizes

Plate 1399.

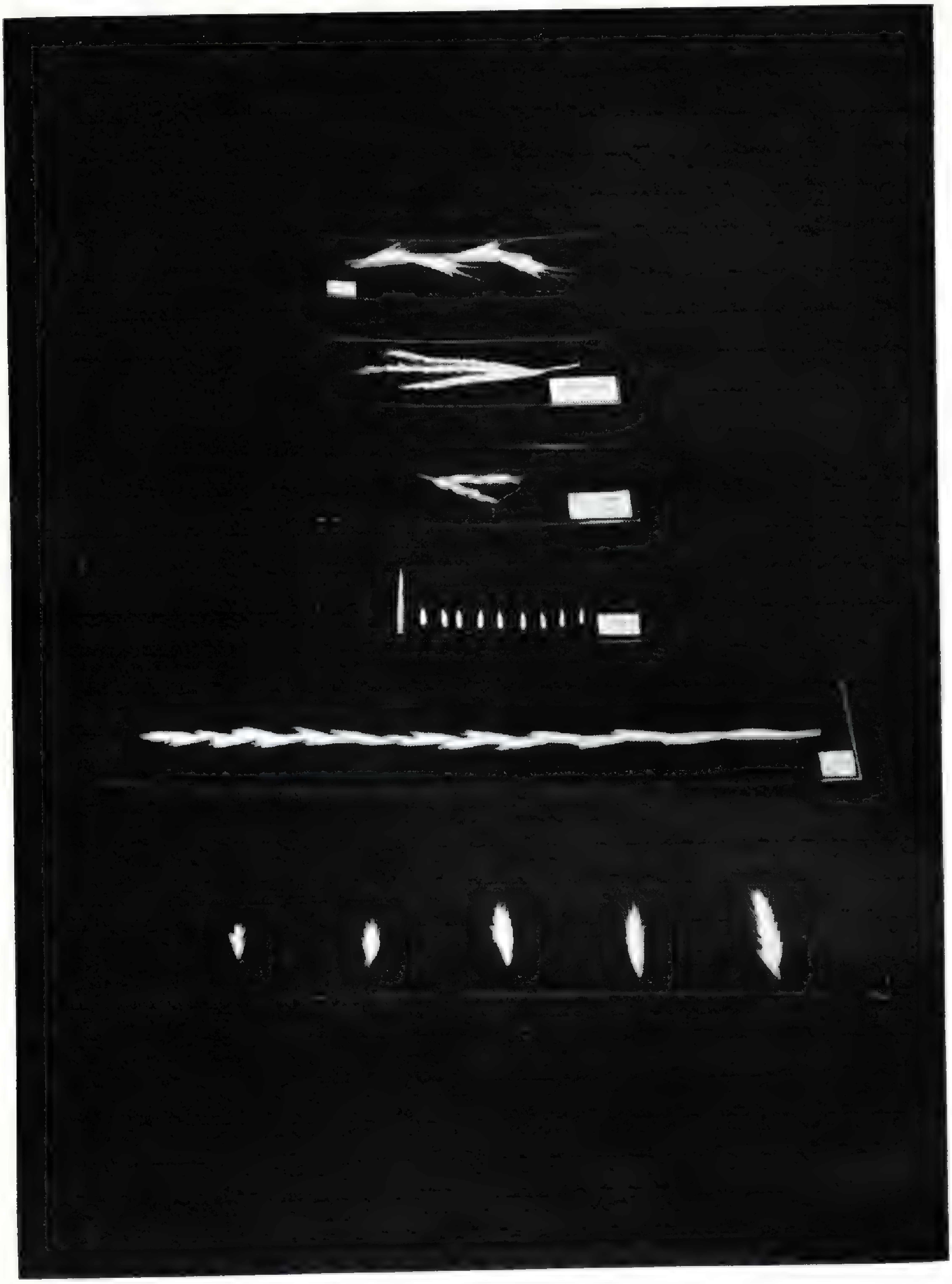

Fig. 1. Plastic slides (3″ × 1″ and 6¼″ × 1″) bearing mounted plant material.

of slides are particularly well-suited for taxonomic studies of grasses and other plants with small reproductive parts.

Transparent cellulose acetate with polished surfaces may be purchased in 20″ by 50″ sheets of various thicknesses. Among the most useful thicknesses are .020″ (0.5 mm.) to .040″ (1 mm.). Commercial "see-thru" rulers are about .020″ thick. At present, the retail costs per sheet are about $4.50 for .040″ and about $2.70 for .020″. Over 300 3″ by 1″ slides may be cut from one of these sheets. There are at least two suppliers of the plastic in the Washington, D. C. area; it is supposed that any large city would have one or more suppliers.

Measurement of Variation

Cellulose acetate is useful in making the measurements needed for the study of hybridization by Andersonian methods and in other kinds of biometrical and numerical taxonomic studies. Three general kinds of uses are possible: (1) slides or pieces of plastic marked with lines, angles, etc. as measuring devices, (2) plant material mounted on plastic for visual comparison, (3) plastic cut into the shape of leaves or other parts after tracing an outline of the part. The first two procedures speed up the mechanics of making measurements and improve objectivity. The third procedure has not been tested, but might be useful if "model" leaves representing typical or other states of variation were needed.

In an investigation of hybridization between two grass species (Terrell, Hovin, and Hill 1965), a plastic device (Fig. 2) was used to measure glume length. The total range of variation in glume length was first established and then divided into class-groups as follows: 1.5-1.9 mm; 2.0-2.4 mm; etc. up to 5.5-5.9 mm. The *upper limits* of class-groups were inscribed on a slide: 1.9 mm; 2.4 mm; 2.9 mm; etc. up to 5.9 mm (such inscriptions rubbed with a red pencil are more easily visible). By overlaying the slide on the samples to be measured the lengths of the glumes were determined as far as the class-groups were concerned. In measuring the samples only "yes-or-no" decisions were

Plate 1400.

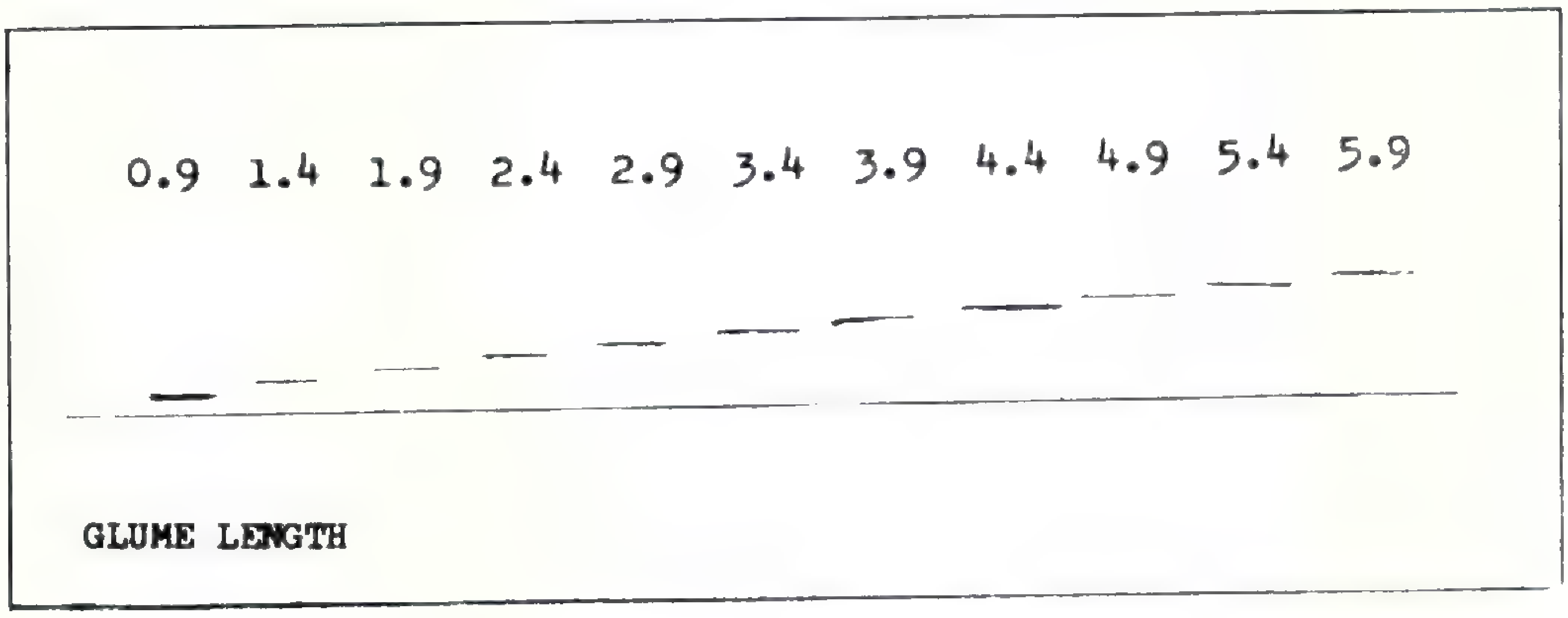

Fig. 2. Plastic device used in measuring length of glumes (see text).

required: if glume lengths in plant 3657-1 were longer than 1.9 mm but shorter than 2.4 mm they fell into the "2.4 group". (The number, 2.4, was circled on a mimeographed sheet previously set up for recording data.) For statistical purposes all glume lengths in the "2.4 group" were assumed to be at the mid-point of this class-group, namely 2.2 mm. This mid-point convention is believed statistically valid, especially in view of the small sizes of the class-groups. By using this convention, graphical and statistical treatments were simplified. However, the important point is that the slide as prepared above permitted faster measuring. Parenthetically, it may be pointed out that the slide actually used could have been inscribed like a ruler but only with class-group lines.

One of the ways in which plastic slides are most useful is in measuring such difficult-to-measure characteristics as density of hairs. Two conventional ways to measure density would be to: (1) use a plastic ruler and count the number of hairs per linear unit; or (2) cut a hole in a piece of

paper, overlay on the samples, and count the number of hairs per unit area. On the other hand, one may mount the actual plant material on plastic slides. As a preliminary, the total range of density present in the plant material studied is divided into equal-sized class-groups. The plants are surveyed to find plant parts with hair densities representing the upper limits of class-groups. Pieces of stem or other plant parts representing the desired states of density are cut and mounted on a plastic slide. Each piece is given a code number for recording of data. Measuring of the samples involves only "yes-or-no" judgments, made instantaneously by visual comparison. Preparation of the completed slide takes longer; but, once prepared, the slide permits faster measurements by eliminating the counting part of the operation, only matching is involved.

There are other difficult-to-define characteristics. It is not easy to put into words or numerical terms degrees of variation in texture of hairs, appression of hairs, or induration of glumes, for example. If the actual plant parts are mounted on plastic, verbal descriptions such as hirsute are defined in terms of the hairs themselves. Once the initial decision is made as to what will be meant by hirsute, the plant part mounted on the plastic becomes a model or standard for all subsequent comparisons. The standard never changes and does not have to be remembered, only preserved. Samples to be measured are judged by visual matching with the objective standards, not with vague concepts held in the mind.

Herbarium and Reference Uses

Slides. Slides bearing mounted plant parts are useful also to the monographer studying a plant group or to the person who wishes to have available a representative critical part of a species as an identification-aid. Two of the slides in Fig. 1 were prepared for the latter purpose; they bear typical inflorescences of *Hyparrhenia rufa* and *Dichanthium annulatum*, introduced grass species. They were labelled with six letters, the first three letters of the genus and species names (e.g., Dicann=*Dichanthium annulatum*). A

Plate 1401.

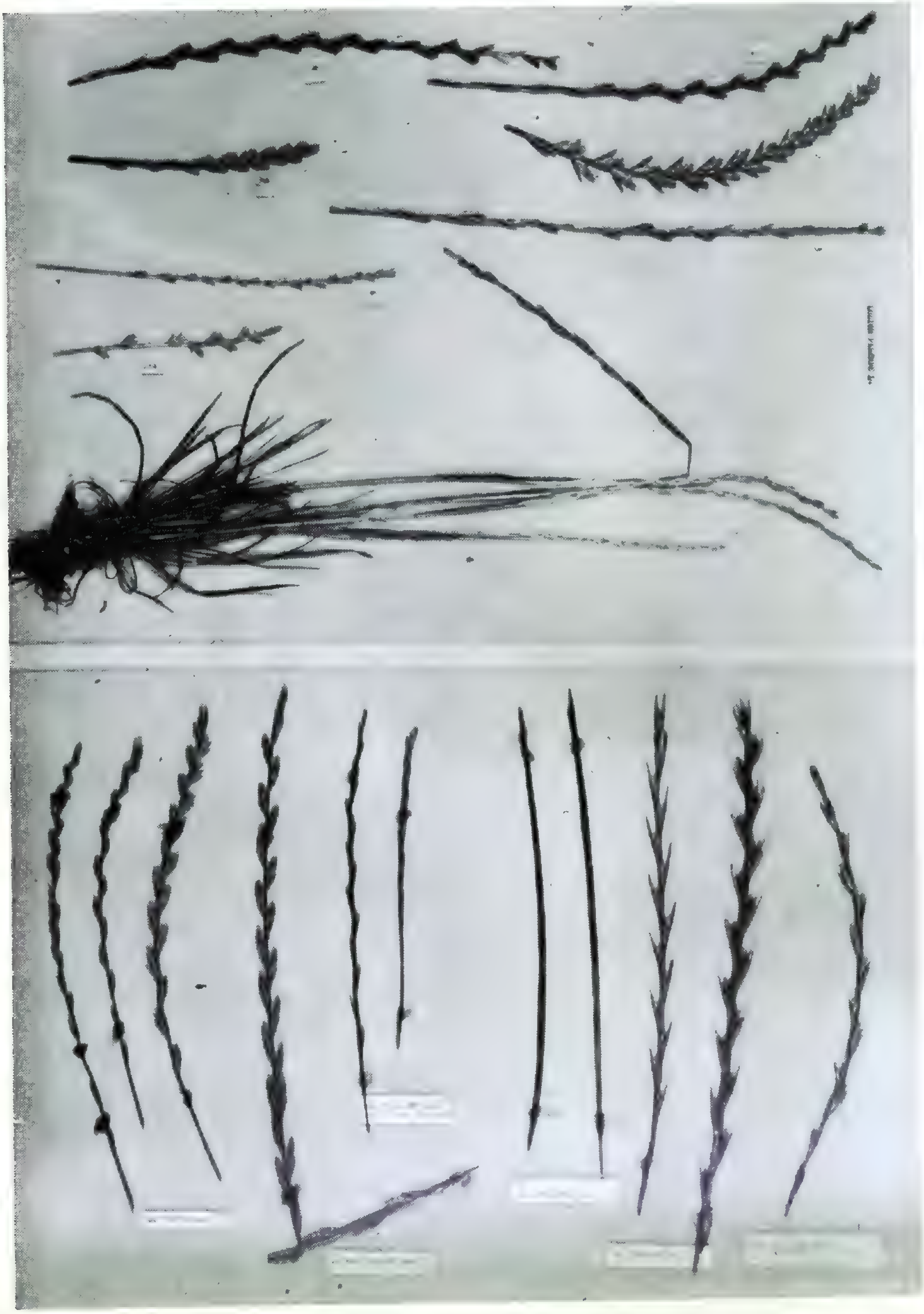

Fig. 3. (above). Plastic herbarium sheet bearing *Lolium perenne* plant and spikes. Fig. 4. (below). Sheet bearing spikes of six *Lolium* species.

number followed, in this case U.S.D.A. PI numbers for specimens from which the inflorescences were obtained. Written records of the source data were kept for each slide.

Herbarium sheets. A plastic sheet 20″ x 50″ may be cut into four standard-sized (11½″ × 16½″) herbarium sheets (with some plastic left over for slides). When used as herbarium sheets the plastic is more expensive; however, the suggestions below assume only limited numbers of plastic herbarium sheets will be used (for example, one or two sheets per species). In mounting plants on plastic sheets, Archer's plastic was found to be satisfactory.

Botanists sometimes prepare one or two typical "certified" specimens of each species in order to have available identification-aids. These specimens may be kept in a special reference herbarium or in separate folders with conventional herbarium specimens. In either event, if the specimens were mounted on plastic instead of paper sheets, it would be possible to make more effective comparisons with unknown specimens. Even persons with good "form memories" have difficulty comparing details of closely related species without seeing them side-by-side. Fig. 3 shows a more or less typical plant plus selected inflorescences to illustrate much of the variation existing in the species, *Lolium perenne*. Similar plastic sheets of other species of the genus would obviously be very helpful aids to identification in a reference herbarium. In Fig. 4 inflorescences of six of the eight species of *Lolium* occupy one sheet. The information-equivalent of six slides, it compresses much information in a small space.

CROPS RESEARCH DIVISION, AGRICULTURAL RESEARCH SERVICE,
U. S. DEPARTMENT OF AGRICULTURE,
BELTSVILLE, MARYLAND 20705

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A REVERSION IN POLYMNIA CANADENSIS (COMPOSITAE) AND NOTES ON THE PEDICELLATE DISK FLORETS IN THE GENUS[1]

EDWIN B. SMITH

While examining a folder of *Polymnia* in our herbarium, I came upon an unusual form of *P. canadensis* L. The specimen is from Polk County, Arkansas *(J. T. Buchholz 245)* and a notation on the label reads "infected with galls." I examined the specimen in detail and found that, while there was evidence in several of the heads of worm damage, the odd appearance of the specimen was due to what has been called a reversion (return to an ancestral condition) of the type exemplified in *Hypochoeris radicata* (Collins, 1921) and, to a lesser extent, in *Taraxacum officinale* (Smith, 1965).

Figure 1 is a diagrammatic comparison of a normal and a reverted disk floret of *Polymnia canadensis.* The reverted florets are characterized by a long pedicel tipped by a somewhat shortened but normally colored corolla, normal (apparently fertile) anthers, and a sterile secondary pedicel (in place of the normally sterile pistil) which bears a pair of bracts and a terminal fascicle of bracts. In the axils of the bracts in the fascicle, secondary reverted florets were developing, producing compound umbels in the most developed ones. Heads on the specimen did not set fruit. The ray florets (normally fertile) in the reverted heads developed in a manner similar to that of the disk florets, but the corolla in these was greenish and somewhat spathe-like (as in *T. officinale;* Smith, 1965). The phyllaries and receptacular chaff in the reverted heads were normal. In some of the less developed disk florets, the secondary pedicel ended at the pair of bracts.

I noticed, when comparing the normal and the reverted florets, that even the normal disk florets of *Polymnia canadensis* have short (ca. 1-3 mm) pedicels, a character to my

[1]The author was the recipient of the NSF Grant GB 6854 during the time of this study.

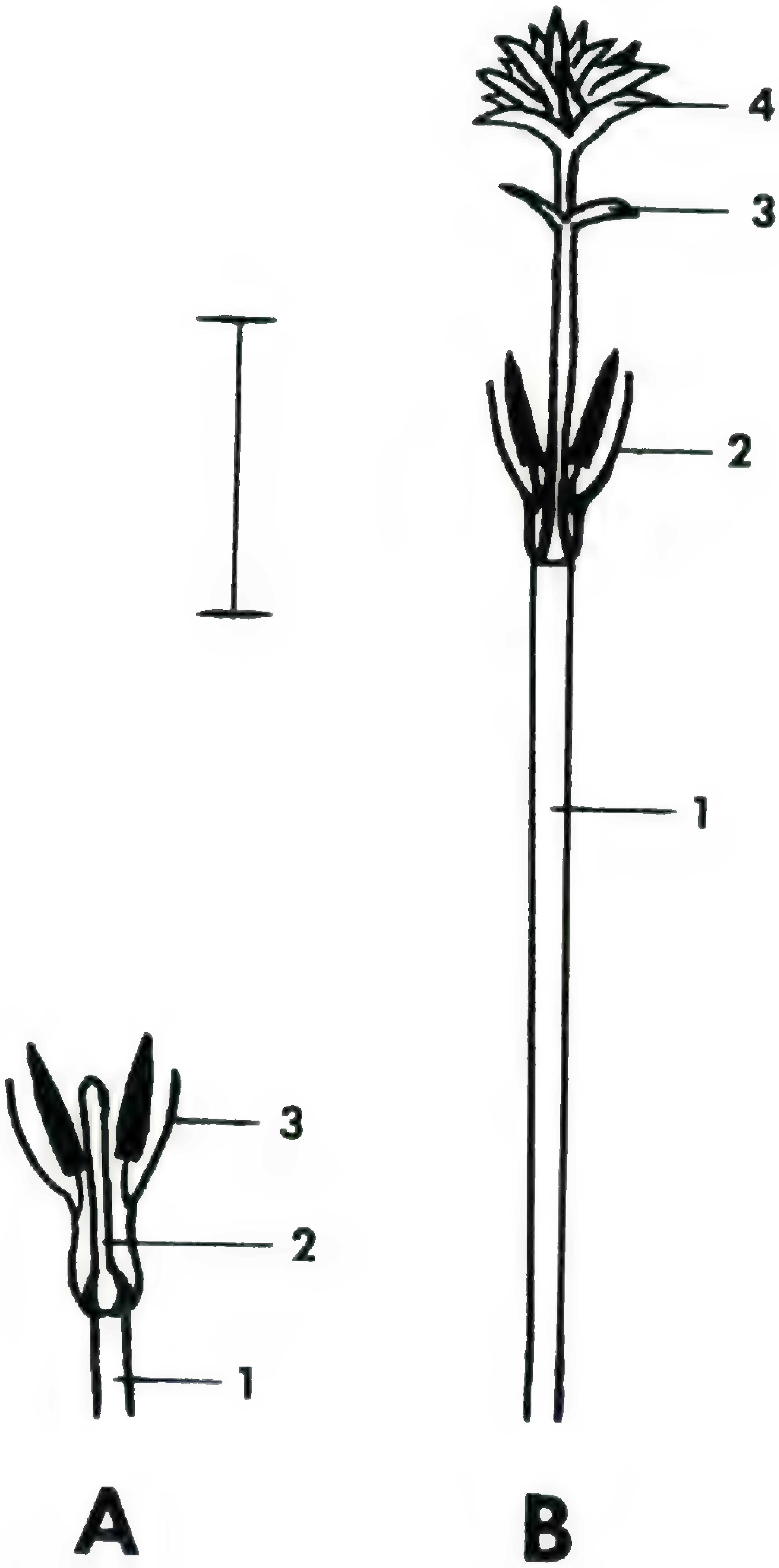

Fig. 1. Diagrammatic longitudinal section of a normal and a reverted disk floret of *Polymnia canadensis* L. Reference line about 5 mm. Anthers are shown in solid black. A. Normal floret: 1 = short pedicel; 2 = sterile pistil with undivided stigma; 3 = whitish corolla. B. Reverted floret: 1 = greatly elongated pedicel; 2 = whitish corolla; 3 = pair of bracts; 4 = fascicle of bracts.

knowledge quite rare in the Compositae. Examination of several specimens of *P. uvedalia* L. disclosed the fact that its disk florets are also normally pedicellate.

I am writing this note for two reasons: firstly, to add *Polymnia canadensis* to the list of species known to exhibit reversion. The close correlation between the morphology of the reverted heads of it and *H. radicata* (Collins, 1921) is striking. Secondly, to point out that the genus *Polymnia* (or, at least *P. canadensis* and *P. uvedalia*) is characterized in the *normal* condition by pedicellate disk florets. This second reason has further significance in two respects.

It would seem worthwhile to include in the description of the genus *Polymnia* in our state and regional floras, the fact that the disk florets are pedicellate. This character alone, I believe, would distinguish the genus from all other Compositae in our area. None of the manuals of use in this area mentions the character (Steyermark, 1963; Fernald, 1950; Gleason, 1963; Small, 1933), but it would seem to merit inclusion as one of particular significance.

The Compositae are believed by many taxonomists to have originated phylogenetically from umbellate ancestors (Collins, 1921; Bessey System, through the Rubiales, as in Core, 1955) by reduction and finally elimination of the pedicels of the umbels. The pedicellate condition of *Polymnia* disk florets supports the theory of the umbellate origin of the Compositae and substantiates the aptness of the term "reversion" for the type of morphological change exhibited in Figure 1. It also marks *Polymnia* with one of the most primitive characteristics in the Compositae.

DEPARTMENT OF BOTANY & BACTERIOLOGY,
UNIVERSITY OF ARKANSAS, FAYETTEVILLE

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A "PILLAR"-TYPE BLACK SPRUCE.

While riding on Route 101-B in Candia, New Hampshire in Dec. 1967 I happened to see what looked like a black pillar or smoke stack in a swamp. Upon investigation the smoke pipe turned out to be a black spruce *(Picea mariana* (Mill)BSP.) about 6 in. in diameter and 35 ft. high with a tightly appressed green crown reaching to the ground. The branches were tightly thatched about the stem. There was no evidence of brooming caused by dwarf mistletoe. The crown was hardly wider than 18 in. at any point. About 10 feet southwest from this tree, (which stood alone, with no other trees of similar height closer than 50 feet) grew a black spruce with almost completely different branching habit. It was barely 5 feet high with a pyramidal crown spreading to a diameter of about 10 feet on the ground. It, too, was densely foliaged. No cones were evident on either tree.

Black spruces with narrow or irregular crowns are common, but I have never seen one with such a narrow cylindrical crown. Mutants with crowns of this form have frequently been reported in *Picea abies* L., in fact I have found some myself in northern Sweden. This phenomenon has been discussed by Sylvén (1909), Rubner (1936) and H. Schmidt (1952) among others. Thus Wahlgren (1922) shows in Fig. 184 a "pillar" spruce from Grönsinka National Forest, Sweden and describes it (p. 477) "with short,

Plate 1402.

Pillar-form of Black Spruce in Candia, New Hampshire

densely interwoven branches along the stem, which give the tree a pillar-form appearance." Bouvarel (1954) pictures a less extreme form which he terms "mutant quenouille" (distaff or bed-post).

Twigs from these black spruces have been sent to University of New Hampshire, Yale and the Arnold Arboretum for propagating.

HENRY I. BALDWIN
HILLSBORO, NEW HAMPSHIRE 03244

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NOTES ON FESTUCA ARUNDINACEA AND F. PRATENSIS IN THE UNITED STATES

EDWARD E. TERRELL

Current regional and state floras of the United States provide varied treatments of the European grasses, *Festuca pratensis* Huds. (*F. elatior* L. of American authors; see Terrell 1967) and *F. arundinacea* Schreb. For example, the eighth edition of Gray's Manual recognizes simply *F. elatior* sens. lat. Gleason in Britton and Brown's Illustrated Flora recognizes var. *pratensis* (Huds.) Gray and var. *arundinacea* (Schreb.) Wimm. under *F. elatior*. Hitchcock's Manual of Grasses (1951 ed.; rev. by Chase) recog-

nizes *F. elatior* and *F. arundinacea* but treats the latter as of limited distribution in the United States. Other floras employ a great variety of characters of variable worth to separate the two taxa. Generally, there is a scarcity of information in the American floristic literature regarding these European taxa.

The purpose of these notes is to point out the following: (1) recent European (or at least British and Scandinavian) floras consider *F. pratensis* and *F. arundinacea* as separate species, (2) several characteristics are ideally available to distinguish the taxa, (3) *F. arundinacea* probably is much more abundant and generally distributed in the United States and southern Canada than current floras indicate.

Festuca arundinacea is generally hexaploid ($2n=42$); however, its variants or related taxa may have $2n=28$ or 70 (e.g., see Malik 1967). *F. pratensis* is diploid ($2n=14$). Both species are indigenous to Europe and Asia, and the former species occurs also in north Africa. Hybrids between the species are usually sterile (Jenkin 1959).

Hackel (1882) divided European representatives of this complex into two subspecies, i.e., *F. elatior* subsp. *pratensis* and subsp. *arundinacea*, each with three varieties. However, in the present state of our knowledge it seems best to recognize two species, following such works as Hubbard 1954 and Clapham et al. 1962. Obviously, this complex needs to be studied by modern methods in all parts of its native range.

Various literature sources (notably Crowder 1953, 1956, Hubbard 1954, Clapham et al. 1962, and Gillet 1964) were searched for characters to distinguish the taxa. All characters were then tried out on European and American specimens in the U. S. National Herbarium (Smithsonian Institution). The result is the key given below, in which the more significant characters are in italics. Well-collected specimens are necessary; even so, some specimens will be more or less intermediate. Hybrids would be expected to have abnormal anthers or sterile pollen. Illustrations of the lemmas are given by Musil 1963 and Gillet 1964. Huon

(1965) indicated that epidermal characters also are useful in separating the taxa.

KEY TO F. PRATENSIS AND F. ARUNDINACEA:

Lemmas glabrous, glabrate, or scabrous only at apex, awnless or rarely short-awned; spikelets cylindrical to narrow-oblong; rachilla internodes glabrous or nearly so; *shorter branch of each pair of panicle branches bearing only 1-2 spikelets;* panicles 10-35 cm. long; *basal leaf sheaths breaking up and often decaying into irregular dark-brown fibers;* leaf blades usually 2-6 (-8)mm. wide; *auricles glabrous;* plants 30-120 cm. high. .... *Festuca pratensis* Huds.

Lemmas scabrous or short-hispid with minute teeth all over or only on nerves or keels (visible at 10 × or more magnification) or rarely glabrate, short-awned (to 4 mm. long) or awnless; spikelets elliptic to oblong; rachilla internodes scabrous; *shorter branch of each pair of panicle branches bearing 3 or more spikelets;* panicles 10-50 cm. long; *basal sheaths tough, whitish to darkish, persistent;* leaf blades 3-12 (usually 4-6) mm. wide, usually stiffer and more heavily nerved than blades of *F. pratensis; auricles ciliolate at least on lower leaves or sometimes glabrous;* plants 45-180 cm. high, usually taller, more robust, and with thicker culms than *F. pratensis.* .... *Festuca arundinacea* Schreb.

Festuca arundinacea (tall fescue) is currently much used in U. S. agriculture especially in the form of its cultivars 'Kentucky 31' and 'Alta'. Tall fescue is extensively sown to prevent erosion along new highways in the southeastern states, Middle Atlantic states, and parts of the Middle West. To some extent it is employed in the same regions also as a forage crop. In the Pacific Northwest it is primarily a seed crop, secondarily a forage crop. *Festuca pratensis* (meadow fescue) is very little used.

The U. S. National Herbarium has about 230 American specimens of *F. pratensis* (as *F. elatior*), many of which were collected more than 50 years ago. In contrast, there are only about 30 specimens of *F. arundinacea,* mostly collected since 1940. Both species occur in all sections of the United States and southern Canada. The scarcity of specimens of *F. arundinacea* is due partly to its having been used extensively in agriculture only in more recent years, and to the natural tendency of many collectors to ignore

roadside plants if they appear to have been planted or sown.

Field observations in the eastern states suggest that *Festuca arundinacea* is much more abundant than many current floras and herbarium specimens indicate. In Maryland and Virginia it is a common feature of the roadside flora and may occur in solid stands for many miles. In eastern North Carolina it was seen also along ditch banks. Smith (1965) found *F. pratensis* (as *F. elatior*) in 26 districts in New York State, *F. arundinacea* in 16 districts. Although the extent to which *F. arundinacea* establishes itself as a weed from seeds is yet uncertain, it must be considered an increasingly conspicuous part of our roadside flora.

CROPS RESEARCH DIVISION
AGRICULTURAL RESEARCH SERVICE
UNITED STATES DEPARTMENT OF AGRICULTURE
BELTSVILLE, MARYLAND

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YELLOW-FRUITED CORNUS FLORIDA — CULTIVAR OR FORM?

ROBERT D. MACDONALD[1]

During the period from August, 1966 through November, 1967 a number of yellow-fruited[2] plants of *Cornus florida* L. were observed in Tennessee. On the basis of these observations, and reports received, it would seem that an adjustment in nomenclature (from *C. florida* cv. Xanthocarpa to *C. florida* forma *xanthocarpa* Rehd.) for this taxon may be warranted.

During October and November, 1967 five spontaneous plants of *Cornus florida* bearing yellow fruit were observed. One plant (No. 1, Table I) was located in Monroe County, one (No. 2) in Anderson County, and three (Nos. 4, 5, and 8) in Knox County. One plant (No. 7) which was grown from seed was obtained from Roane County, but the seed source (possibly Warren County) is unknown.

Occasional yellow fruits have been reported as being found in large amounts of fruit purchased by commercial nurserymen in Warren and Franklin Counties. This fruit reportedly is collected by local residents from spontaneous trees. These reports are from reliable sources but have not been personally verified. A report was received from a

[1]Director, John J. Tyler Arboretum, Lima, Pennsylvania 19060.

[2]2.5 Y 8/12, vivid yellow to 10 YR 8/10, moderate orange yellow (color notations are taken from the Nickerson Color Fan with Munsell hue color symbols).

forester of a spontaneous yellow-fruited plant growing in Campbell County. This report was not personally verified.

The only record of a yellow-fruited plant of *Cornus florida* contained in the University of Tennessee Herbarium is that of a plant (origin unknown) in Knox County. This is sheet No. 6997 collected by Dr. C. Rappennecker, November 24, 1948. This plant could not be located.

Spontaneous plants with yellow fruit were reported in Swain County, North Carolina, on Hazel Creek near the Tennessee State Line, but these plants have not been personally verified.

It is my observation that, on the basis of fruit color alone, it is impossible to distinguish the plants in the trade (cv. Xanthocarpa) from the spontaneous yellow-fruited plants.

It has been determined that the difference in color between the red and yellow fruits of *C. florida* is due to the complete absence of two anthocyanins (peonidin and petunidin) in the exocarp (Chester and Stone, 1964). The origin of the material analyzed was not given.

The yellow-fruited forms of *Cornus florida* L. would appear to now enjoy only cultivar status. Howard (1961) in his list of cultivar names in *Cornus* lists (under *C. florida*), " 'Xanthocarpa' (Rehder, Jour. Arnold Arb. 2: 179. 1921).[3] Distinct on the basis of the yellow fruit. Described from material collected in Saluda, North Carolina in 1919."

Howard (1967) states, "A yellow-fruited *Cornus florida* has also been found near Oyster Bay, Long Island, by Hicks & Co. of Westbury." Howard further indicated, "The herbarium supports the idea that both the Wilcox [material from Saluda, North Carolina] and Hicks specimens came from plants under cultivation." Howard mentioned, in addition, that his notes show no specimens of spontaneous plants with yellow fruit were found in the herbarium of the New England Botanical Club, the Gray Herbarium, or the Arnold Arboretum herbarium.

The International Code of Nomenclature for Cultivated

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[3]Rehder described this taxon as a *forma (Cornus florida* L. f. *xanthocarpa, forma nov.).*

Plants (1961) states (Article 5), "The term cultivar . . . denotes an assemblage of cultivated individuals . . .". The category *forma* is generally applied to trivial variations occuring among individuals of any population. Fruit color is an example of such variation.

Howard (1961) states, in respect to *Cornus florida* cv. Rubra, "This name should not be used as a cultivar. Although Weston described it on the basis of cultivated material, the plant is known in the wild from pre-Linnean references as well as from modern observations and has been treated as *Cornus florida* forma *rubra* (Weston) Palmer and Steyermark."

It is my opinion that yellow-fruited plants of *Cornus florida* should be treated as forma *xanthocarpa* Rehd. The name should not be used as a cultivar, since the statement which Howard (1961) applies to *C. florida* cv. Rubra may (for the most part) be applied here.

Table I. Observations regarding yellow-fruited plants of *Cornus florida*.

Herbarium Collection No.[1]	Origin of Plant	Height	Diameter[2]	Location (Tenn.)
COFL-XA67-1	Spontaneous	8′	2″	Monroe Co.
COFL-XA67-2	Spontaneous	12′	5″	Anderson Co.
COFL-XA67-3	Commercial Nursery	5′	Two small stems	Knox Co.
COFL-XA67-4	Spontaneous	12′	4.5″	Knox Co.
COFL-XA67-5	Spontaneous	18′	4″	Knox Co.
COFL-XA67-6	Commercial Nursery	6′	Four stems 1″ to 2″	Knox Co.
COFL-XA67-7	Commercial Nursery	18″	<½″	Roane Co.
COFL-XA67-8	Spontaneous	14′	3″	Knox Co.

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[1]Author's personal collection.

[2]Diameter measured 4½ feet above ground.

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OCCURRENCE OF MURDANNIA SPIRATA IN FLORIDA[1]

The recording of a description of this species in American botanical works is deemed important because of its extended distribution from the Asiatic tropics of the Eastern Hemisphere to the subtropics of the Western Hemisphere. According to Dr. J. P. M. Brenan who determined the specimen, the discovery is the first one out of its native region.[2]

Murdannia spirata (L.) Bruckner. (*Aneilema spiratum* R. Br.) Plant annual, to 3 dm long; stems slender, soft, ascending, rooting at nodes, diffusely branching in age, glabrous, only the internodal groove viscid-villous; leaves thin, acute, 2-4 cm long, 4-10 mm wide, lanceolate, white-margined; the cordate-rounded clasping base sparsely ciliate or glabrate; inflorescence terminal or axillary, few-flowered, in axils of the uppermost leaves; peduncle elongate usually forked into 2, flexuous, divergent, paniculate branches; pedicels 5-9 mm long, distant, subtended by small, acute, clasping, floral bracts; living flowers in full anthesis 4-6 mm long; sepals concave greenish, diffused with pink; petals 4.5-5.5 mm long, pinkish-lavender; limb suborbicular veined in deeper shades, minutely cremate-denticulate at apex, clearly showing 3 vascular traces forking and reforking into finer traces radiating toward the

[1]Contribution No. 33 from the Botanical Laboratories, University of South Florida. Aided by grant GB-2742 from the National Science Foundation.

[2]The author is deeply indebted to Dr. J. P. M. Brenan for his determination of the species.

Plate 1403.

Murdannia spirata

margin; stamens opposite the sepals; anthers pastel blue, pollen white; individual grains colorless oval-oblique in face view; filaments tapering to anther connectives from thicker barbate base; hairs beaded; staminodes white, 3-lobulate; style 3 mm long, stigma capitate; capsule ovoid with tardily deciduous style; valves lustrous, chartaceous, apex with persistent style base; seeds angled, averaging 0.8-0.9 in length, typically 4, uniseriate in each locule, contiguous surfaces truncate, the first and the last rounded at free ends; testa pale gray, sparsely verrucose.

Murdannia spirata differs from *M. nudiflora* in softer texture of the plant as a whole; leaf-shape; finer pubescence; diffuse, paniculate inflorescence; blue anthers; color of the petals; more numerous, smaller seeds.

The known distribution in Florida is restricted to northern Collier County, in the vicinity of Immokalee. A population of this plant was first noted on the margin of a seasonally wet prairie glade, 6 miles north of Immokalee. The lush green plants dispersed in mucky soil among tufts of *Eleocharis* and *Hydrocotyle* presented a different appearance from *Murdannia nudiflora* (Coll. *Lakela 29185*, Oct. 5, 1965, in flower and fruit).

The plants were encountered in anther site at Immokalee City limits. The colony was centered in a hollow of sand, made by upturned roots of a fallen pine. Over the area on a road off the main street, *Pinus Elliottii* and *Sabal palmetto*, remnants of pine flatwoods, cast an open shade. The plants filled the hollow completely and were largely post-mature but still in excellent fruit. Photo. (Coll. *Lakela 29412*, Jan. 6, 1966.)

These sites were conveniently located for follow-up study and collecting. The period of anthesis is approximately from September-December. Flowers remain open for from two to three hours. Duplicates of dried specimens with one living plant were mailed to Kew, England.

OLGA LAKELA
UNIVERSITY OF SOUTH FLORIDA
TAMPA, FLORIDA 33620

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EMENDATIONS IN UNITED STATES PHYSALIS

U. T. WATERFALL

An investigation of *Physalis* in Mexico, Central America and the West Indies, undertaken during the past four years, including a trip in August, 1965 to study types and other historically significant specimens in European herbaria, has resulted in the necessity of reinterpreting some of the taxa of this genus in the U.S. In addition, further observation indicates the desirability of a change in status for another taxon.

Physalis hederaefolia Gray, var. **puberula** Gray was included in var. *hederaefolia* in the earlier treatment (Waterfall, 1958). In studying Mexican material it seemed that collections with vesiture of short, antrorse hairs only, or with varying amounts of glandular-capitate trichomes, might well be referred to var. *puberula*, those with vestiture including long, jointed hairs to var. *hederaefolia* (Waterfall, 1967). The two may be intermixed in much of their range, but var. *puberula* is more western.

Examples of var. *puberula* include: CALIFORNIA: SAN DIEGO CO.: *"Cleveland collection" 6993*, between Walkers and Jacumba, June 23, 1885 (SD); *Daniel Cleveland 6931*, July 3, 1884 (SD); ARIZONA: COCHISE CO.: *Wyatt W. Jones sin num*, Don Luis, Aug. 18, 1956 (SD); YAVAPAI CO.: *Charles W. Harbison 41.220*, Kirkland Junction, May 29, 1941 (SD).

Physalis philadelphica Lamarck, var. **immaculata** Waterfall, Rhodora **69**: 215. 1967. This small-flowered variety

with essentially immaculate corollas was described from Chihuahua, Jalisco, Guanajuato and Sonora.

Specimens at hand from the United States are: ARIZONA: COCHISE CO.: *Booth & Jones sin num*, Don Luis, Aug. 26, 1955 (SD); *Wyatt Jones sin num*, McNeal, Sept. 6, 1962 (SD).

Physalis cordata Miller includes the material with large, glabrous, acuminate-toothed fruiting calyces originally referred by the author (1958) to *P. pubescens* var. *glabra* which proves to be only an extreme of *P. pubescens* var. *pubescens* (Waterfall, 1967).

Representative collections at hand are: ARKANSAS: HOT SPRINGS CO.: *Demaree 30279*, foothills, Magnet Cove, Butterfield, Oct. 28, 1950 (OKLA); CALIFORNIA: SAN DIEGO CO.: *Gardner 9820*, Lakeside, Sept. 26, 1945 (SD); FLORIDA: POLK CO.: *J. Cecil King sin num*, Lake Wales, Sept. 3, 1958 (OKLA); LOUISIANA: ASCENSION PARISH: *Anna Ashby 36*, very frequent in cane field, 4 miles from Donaldsonville, Nov. 23, 1956 (OKLA); LA FOURCHE PARISH: *Joseph Ewan 18877 pro parte*, S. P. RR. Station, Raceland Junction, Oct. 20, 1956 (OKLA).

Physalis turbinata Medicus has longer, narrower calyx lobes, and larger fruiting calyces than *P. pubescens sens. str.* to which it is closely related (Waterfall, 1958). Much of the material labelled *P. turbinata* in American herbaria is *P. cordata* Miller, a glabrous, or near-glabrous species with long fruiting pedicels, quite different from the hairy species specified by Medicus.

Representative collections at hand are: FLORIDA: POLK CO.: *McFarlin 5924*, Bartow, June 23, 1931 (CAS); TEXAS: ANGELINA CO.: *Hamby 1582*, 3 mi w of Diboll, Aug. 9, 1940 (US); BOWIE CO.: *Correll 31272*, hardwood hills, among grasses in open woods, about 2 miles north of Texarkana, July 12, 1965 (LL); CAMERON CO.: *Correll 14856*, La Palmas Plantation, about 4 miles southwest of Brownsville, in palm grove, Oct. 4, 1952 (LL); HARRIS CO.: *Correll 31889*, in rich woods of meadow along stream near Addicks, Oct. 6, 1965 (LL); HIDALGO CO.: *Fleetwood 3112*, Santa Ana National Wildlife Refuge south of Alamo, Sept., 1959 (TEX); WILLACY CO.: *Johnston 542221*, sparse mesquite brush over sacahuiste, 9 miles west of Redfish Bay, Nov. 28, 1954 (LL).

Physalis pubescens L., var. **missouriensis** (Mackenzie & Bush) Waterfall, comb. et stat. nov., *P. missouriensis* Mackenzie & Bush, Trans. Acad. Sci. St. Louis **12**: 84-85. 1902.

This taxon seems easily differentiated from *P. pubescens* var. *pubescens* by its immaculate corolla and smaller anthers. Nevertheless, the relationship seems close enough that it might be better to consider it a variety of that species.

DEPARTMENT OF BOTANY AND THE RESEARCH FOUNDATION
OKLAHOMA STATE UNIVERSITY
STILLWATER, OKLAHOMA

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ALISMA GRAMINEUM IN VERMONT

WM. D. COUNTRYMAN

Although common in the western United States north of the 40th parallel and in the adjacent Prairie Provinces of Canada, *Alisma gramineum* K. C. Gmel. has been known in eastern North America only from the St. Lawrence River valley and the eastern end of Lake Ontario.

Asa Gray was apparently the first person to collect *Alisma gramineum* east of the Mississippi River. His specimen, collected at Ogdensburg, St. Lawrence County, New York, is deposited in the Gray Herbarium; unfortunately the label bears no date and, therefore, it can be stated with certainty only that it was collected before January 1888, the date of Gray's death.

In Canada, Brother Marie-Victorin collected the species near Longueuil and at Montreal, Quebec in 1918. Fernald and Wiegand (1923) reported the plant from a cove of Lake Ontario near Chaumont, Jefferson County, New York. Muenscher and Maguire (1931) and Muenscher (1932) found it growing at a number of stations along the St. Lawrence River in St. Lawrence and Franklin Counties, New York. More recently Raymond and Kucyniak (1948) have reported *Alisma gramineum* as "a pesky weed around Montreal . . . . . now progressively invading the Richelieu River Valley."

Such a rapidly spreading species could soon be expected to make its appearance in the Champlain Valley. It is not surprising, therefore, that I found it in Vermont growing along the shore of Lake Champlain at Shelburne Bay in 1961. Subsequent collections have shown it to be present along the shores of the Lake as far south as the Town of Addison, Addison County, Vermont. It is noticeably more common in the northern portion of the lake. In 1966, after diligent searching, I found only a few plants in Addison, Vermont and none at all south of that town. I have not collected on the New York side in the northern portion of Lake Champlain and do not know if *Alisma gramineum*

grows there; it would seem most probable that it does.

Recently I have been privileged to examine the specimens of *Alisma gramineum* in the herbarium of the Plant Research Institute, Department of Agriculture, Ottawa. These collections show that the species is well established on the Canadian side of the St. Lawrence River from Lake Ontario as far downstream as St. Angèle de Laval, Quebec, a distance of approximately 250 miles. Although the plant has now successfully invaded the Richelieu River and Lake Champlain it is interesting to note that it has not yet been found in any other tributaries of the St. Lawrence.

Both submersed plants with ribbon-like leaves and emersed plants with lanceolate to elliptic blades were found at most of the Vermont stations. When fruiting, *Alisma gramineum* is easily recognized by its tricarinate achenes in contrast to the bicarinate achenes of *A. triviale* Pursh and *A. subcordatum* Raf.

All of the specimens cited below were collected by me in western Vermont along the shores of Lake Champlain. I have deposited duplicates of all specimens cited in the herbarium of the New England Botanical Club.

ALISMA GRAMINEUM K. C. Gmelin. VERMONT. GRAND ISLE COUNTY: Alburg, occasional, submersed in bay north of Rouse's Point toll bridge, 11 August 1964 *952*; Isle La Motte, Jordan Bay, 10 August 1964 *948*; North Hero, rare, near North Hero Station, 27 August 1965 *1359;* Grand Isle, Simms Point, The Gut, terrestrial specimens blooming earlier than those growing submersed, 14 August 1964 *958*; CHITTENDEN COUNTY: Colchester, west of R.R. tracks, Colchester Point, 5 October 1964 *1161*; Shelburne, Shelburne Bay, 11 August 1961 *98*; Charlotte, sandy shore at Town Farm Bay, 30 July 1965 *1323*; ADDISON COUNTY: Ferrisburg, occasional at Basin Harbor, 18 August 1966 *1547*; Panton, Arnold Bay, 13 September 1964 *1086*; Addison, scarce, only about 12 plants seen in one-half mile of beach, Potash Bay, 21 August 1966 *1555*.

DEPARTMENT OF BIOLOGY
NORWICH UNIVERSITY
NORTHFIELD, VERMONT 05663

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VOLUME 70
1968
Errata for RHODORA

p. 32 line 12, 15 should be 16.
p. 32 line 12 *mucronota,* should be *curtipendula.*
p. 33 line 20 for *Flagelliformis,* read *flagelliformis.*
p. 43 line 31 for *Astralagus,* read *Astragalus.*
p. 52 line 8 delete the quotation marks before the word Nuttall.
p. 53 line 41 read Ownbey for Ownby.
p. 39 line 5 for *Catesboei,* read *Catesbaei.*
p. 61 caption figs. 9-16 line 1 *Lasioneuron,* should be *lasioneuron.*
p. 72 line 7 for liguils, read ligules.
p. 75 caption fig. 22 line 2 *Illinoensis* should be *illinoensis.*
p. 75 line 1 Smilax illinoensis should be in italics.
p. 101 line 22 Virginica should be virginica.
p. 135 line 7 for yonger, read younger.

No. 782

p. 165 line 2 gracillima should be in italics.
p. 170 line 35 for acquatic, read aquatic.
p. 176 line 6 for *aerolata,* read *areolata.*
p. 202 line 29 for Brauni, read braunii.
p. 207 line 12 *warnstorifianum* should be *warnstorfianum.*
p. 212 lines 1, 11, 12, 26 for Sasketchewan, read Saskatchewan.
p. 225 line 37 for dichotomous read dichotomus.
p. 232 line 7 for *squammatus,* read *squamatus.*
p. 233 line 29 for Cichoreae read Cichorieae.
p. 236 lines 31, 34 for *vellutinum,* read *velutinum.*
p. 286 line 24 for *Banhinia,* read *Bauhinia.*
p. 308 line 9 for woud, read would.

No. 783

p. 394 line 26 for enedmic, read endemic.
p. 401 line 37 for *Talinumm engesii,* read *Talinum mengesii.*
p. 405 line 32 for allopolploidy, read allopolyploidy.
p. 405 line 37 for *teretrifolium,* read *teretifolium.*
p. 414 line 38 for rachus, read rachis.
p. 430 line 23 for apears, read appears.
p. 431 line 19 for *ludoviviana,* read *ludoviciana.*
p. 443 line 29 for *halopila,* read *halophila.*
p. 443 line 31 for *Scripus,* read *Scirpus.*

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